DEPARTMENT OF MARINE BIOLOGY
OF
THE CARNEGIE INSTITUTION OF WASHINGTON
ALFRED G. MAYER, Director

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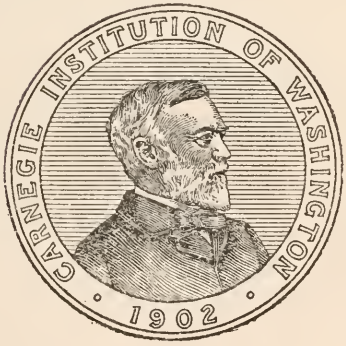
# PAPERS
# FROM THE DEPARTMENT OF MARINE BIOLOGY
OF THE
CARNEGIE INSTITUTION OF WASHINGTON

VOLUME XII

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I.

# SOME AMPHIBIANS AND REPTILES FROM PORTO RICO AND THE VIRGIN ISLANDS.

By HENRY W. FOWLER,

Of the Academy of Natural Sciences of Philadelphia.

One plate, six figures.

# SOME AMPHIBIANS AND REPTILES FROM PORTO RICO AND THE VIRGIN ISLANDS.

By Henry W. Fowler.

The animals comprising the above-named groups were largely obtained in Porto Rico during the early summer of 1915 by Mr. Charles F. Silvester, while on the staff of the expedition of the Carnegie Institution of Washington. They form an interesting accession to the Museum of Princeton University. Another collection, obtained in the Virgin Islands in 1876 by Mr. A. D. Brown, has been studied in this connection and included in the present report. It is also the property of Princeton University. I am under obligations to Mr. Silvester for the opportunity to study all this material, as well as for various notes, information, etc., kindly placed at my disposal. A series of specimens has been reserved for the Museum of the Academy of Natural Sciences of Philadelphia.

The herpetology of Porto Rico has been so ably discussed by Dr. Leonhard Stejneger, in his paper of that title, published in 1902, that the present account is intended as merely supplementary.

## AMPHIBIA.

### LEPTODACTYLIDÆ.

**Leptodactylus albilabris (Günther). Figure 1.**

Ten from the junction of the Arecibo and Tanama Rivers, Porto Rico, on June 9, 1915. As considerable variation in color is noticeable, 5 examples have been selected as an illustration of the dorsal aspect. Two adults show a strongly contrasted color-pattern above, largely of longitudinal bands, of which the median or vertebral is whitish, edged on each side by a blackish band of variable width in places; these blackish bands largely alike. Sometimes a whitish vertebral band gives off a branch on each side in the front interorbital region, which extends over eyelid. Blackish band on each side of snout, including nostril, to eye, then continued behind to embrace tympanum to shoulder, present in all examples. Side of each lip dusky. Several blackish spots on groin and a few obsolete dusky markings along the side. Upper surface of hind limbs strongly contrasted with blackish crossbars. Other examples show lengthwise bands on back obscure, or as irregular blotches, and along the sides as broken small spots. They often form two large Λ-shaped obscure blotches on back before pelvis. Two dark lateral bands may unite in hind interorbital region to form a connecting dark bar. Some examples have the throat dusted with pale dusky, though in most the entire under surface is uniform whitish.

One metamorphosing example and several tadpoles from Utuado; a small example from the Virgin Islands. The Porto Rican examples were obtained along small streams flowing into the Arecibo River about 5 kilometers south of Arecibo, where the lowlands merge into the hills. Active during day-time.

**Eleutherodactylus auriculatus (Cope). Figure 2.**

Collected 21 examples from the junction of the Arecibo and Tanama Rivers on June 9. This little amphibian is extremely variable in color. Some individuals are pale or very light, others dark, and some of all ages with a narrow whitish vertebral line. Four extremes of color-variation are represented in the accompanying figures of the dorsal surface.

All the examples with the narrow whitish vertebral line (4 individuals) show it bifurcate and extending out on each side of the hind femoral surface toward the under surface of the knee. The larger of these examples are also

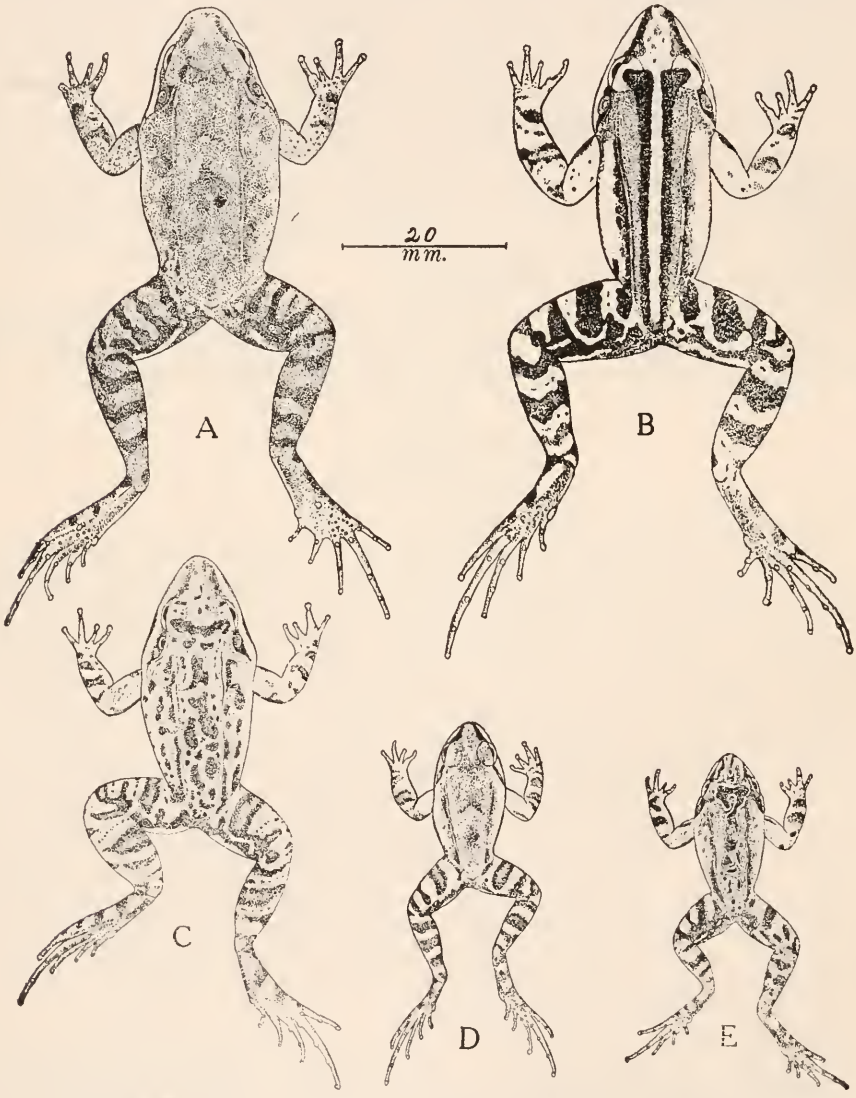


FIG. 1.—*Leptodactylus albilabris* (Günther). A to E, variation in dorsal color—pattern of examples of all ages from Arecibo and Tanama River Junction.

irregularly spotted or blotched with whitish on the back, about the interorbital region, and at each heel. A few spots may also occur elsewhere on the upper surfaces of the tibial regions. The smaller examples have large obscure blotches of slightly darker shade than the general color of the upper surface, which tend to form obscure bars across the tibial and femoral regions. The lower body-surface is similarly variable, from slightly soiled brownish to more or less completely marbled with smutty, in which case there is also a median obscure pale line from the chin to the sternum, with line given off each side to the axillaries.

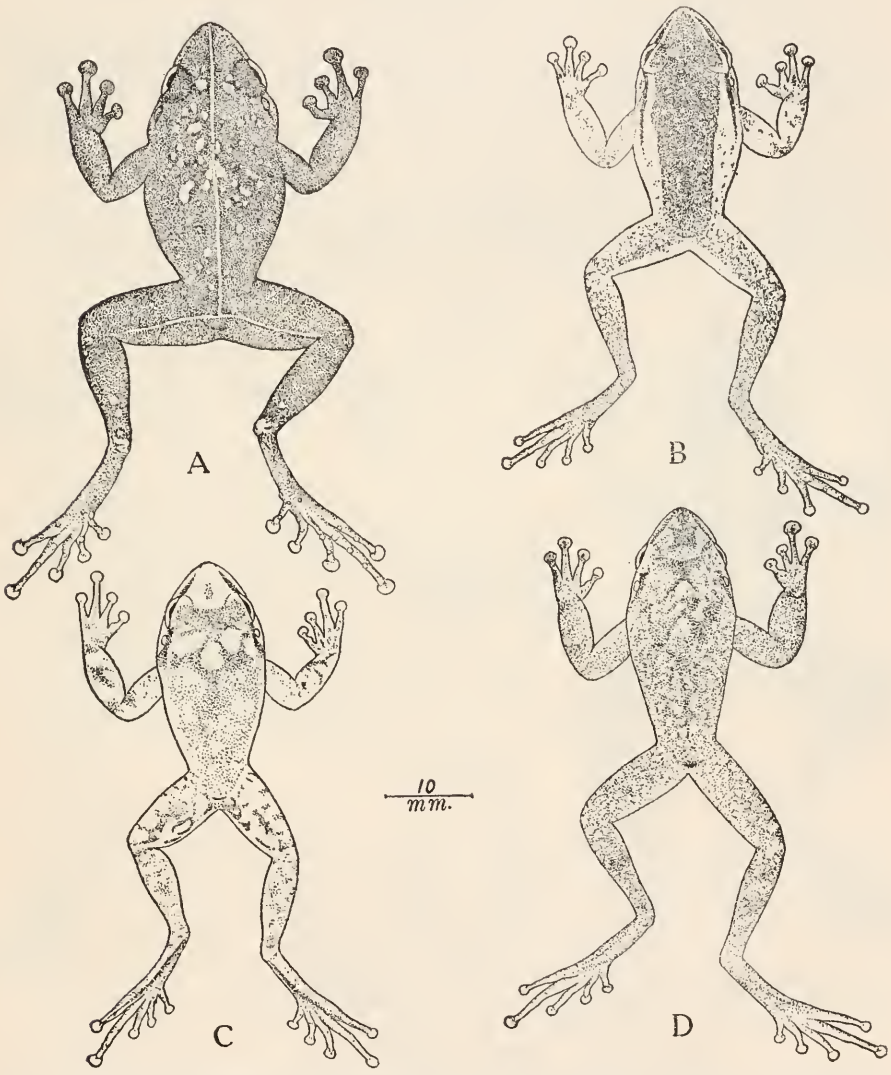


Fig. 2.—*Eleutherodactylus auriculatus* (Cope). A to D, variation in dorsal color—pattern of adult examples from Arecibo and Tanama River Junction.

Four pale examples are also quite variable. One has the front and hind surfaces of the femoral region with rather large dusky vermiculations strongly contrasted with whitish. In this individual there is also a dark-gray interorbital band. Another shows a number of whitish spots on the middle of the back with broad whitish band back from each eye to groin. The lower surface of the body is often uniform whitish.

Large darker olive or brownish examples are more or less uniform in color, though one shows pale areas back from the eye to the groin. They usually have the right and front femoral regions and groin finely speckled brownish on pale ground-color. Most are more or less smutty below.

In a number of small darker examples traces of the light areas back from the eye are seen in two cases and in one of these an accessory short inner line backward and parallel is also present, while the larger bands tend to converge at the middle of the back. All have the limbs above with more or less obsolete dark cross-bars. A dark interorbital band is also usually in evidence.

All examples have the dark line from the eye over the tympanum distinct.

**Eleutherodactylus lentus (Cope). Figure 3.**

Twenty-one examples from the Virgin Islands. These agree with Meerwarth's figure of *Hylodes lentus*,[1] based on examples from St. Thomas. The

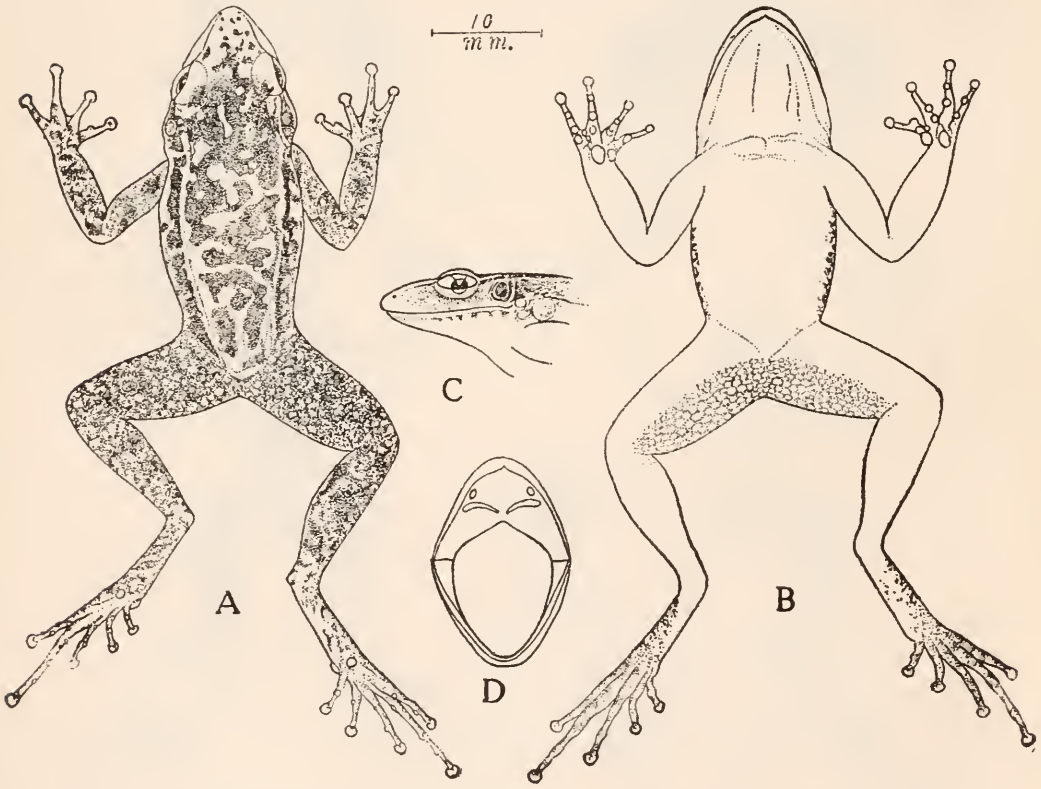


Fig. 3.—*Eleutherodactylus lentus* (Cope). From Virgin Islands. A, dorsal surface. B, ventral surface. C, side view of head. D, open mouth, showing tongue and roof of mouth.

[1]Mitth. Naturh. Mus. Hamburg, xviii, 1901, p. 38, pl. 2, figs. 1, 2.

species appears to be less variable than many of this genus. Although Cope states that the body "is without granulations above, below, or upon the sides," all my examples show them on the lower hind femoral region. As Meerwarth's figure lacks detail I have made the following note. In this species the color-pattern is largely constant. Sometimes the blotches or vermiculations are larger and fewer on the back anteriorly, or they may vary in being finer and more numerous, though the general appearance is similar.

## REPTILIA.

### GEKKONIDÆ.

**Hemidactylus mabouia (Moreau de Jonnes).**

Two from the Virgin Islands. According to Dr. Barbour,[1] it was probably introduced into the West Indies.

**Sphærodactylus grandisquamis Stejneger.**

Three from the Arecibo Road, Porto Rico, about the 70-kilometer post, on June 14; these are similar to Dr. Stejneger's figure,[2] except that the black scapular blotch has in each example two small pure white spots. Two specimens have the dark spots as more or less broken longitudinal bands, though in the remaining example a more speckled appearance is seen and the spots are smaller.

Though only the above examples were secured, this gecko was probably abundant at this locality. They were found under stones and sticks in moist places. Their tails were very brittle and were easily broken off.

### SCINCIDÆ.

**Mabuya sloanii (Daudin).**

Two from the Virgin Islands. One shows at least two pairs of chin shields in contact. Color in alcohol largely grayish olive above, paler or whitish below. From each side of the fronto-nasal plate a brown band extends back, including the upper eyelid, and becomes obscure toward the groin, though on front of body in strong contrast, due largely to darker brownish marginal lines. Another band of similar color extends from the nostrils back, including eye, over ear and shoulder, and fades out on groin. Limbs above with obscure brownish spots. Snout to vent 76 mm., tail 66 mm.

This species is now rare in Porto Rico, a circumstance believed to be due to the mongoose.

### IGUANIDÆ.

**Anolis cuvieri Merrem.**

One from Utuado, 405 mm. in total length. Color in life with iris brownish yellow, a ring of pure yellow next to the black pupil. Scales around eye yellow, barred with black. These colors seem to hold even when the animal changes color from black to green and yellow. In alcohol the color is largely uniform bluish above and paler below. Pale crescent below eye.

Known to the natives as "the devil." They are afraid of this species and believe that it is deadly poisonous. Mr. Silvester informs me it is rare and occurs along water-courses. He saw another example along the main course of the Arecibo River at Utuado, but was unable to capture it.

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[1]Mem. Mus. Comp. Zool., XLIV, No. 2, 1914, p. 222.
[2]Rep. U. S. Nat. Mus., 1902, p. 605, fig. 52.

**Anolis mayeri sp. nov. Figure 4.**

*Description.*—Body long, rather robust, with slight dorso-nuchal fold. Head rather level on top, with broad median depression on prefrontal region. Slight median depression on occipital region. Eyelids granular. Teeth moderately large, and become enlarged posteriorly or below eye, those in front of each jaw small. Dewlap moderate, covered with small imbricated scales. Interorbital slightly convex. Ear-opening circular, deep.

Scales all smooth, rather large. Median or vertebral row of scales down back slightly enlarged, and progressing down sides scales become granular on latter. Very minute granules seen scattered about between scales of back, though not visible to the naked eye and not preventing their imbrication on one or more sides in most cases. Scales on belly larger than most scales on back, and small on under surface of head. Scales on head above rather large and smooth. Supraoculars large, flat, and separated from supraorbital semicircles by narrow, complete row of small scales. Supraorbital semicircles with one or two median plates in contact, and separated from occipital plate by one or two rows of scales. Occipital large, nearly equals ear-opening, and scales around variably large and small. Counting vertically, six rows of loreal scales present, and of more or less uniform size. Six or seven large infraorbitals, last ending well before hind edge of eye. Temporals moderate, and about 12 scales between hind eye-edge and ear.

Limbs rather robust. Scales on upper sides of fore-limbs larger than those on middle of back, slightly keeled, and closely imbricated. Scales along lower front femoral region larger than those on belly, smooth and closely imbricated. Scales on upper surface of femur very small and imbricated. Post-anal plate moderate.

Tail strongly compressed, largely with slight crest. Scales covering sides of tail flat, keeled, those in crest longest and enlarged, a keel forming front edge of each.

Color largely uniform brownish in alcohol, paler below. Some very obscure markings on back, upper surfaces of limbs and tail. Slight pale streak from eye through ear and backward. Another from over shoulder and backward.

Total length 188 mm. (caudal tip damaged) and length from snout tip to vent 67 mm.

Type No. 3151, Princeton University, and 7 paratypes. Virgin Islands.

These examples suggest in many ways that they may be the young of *Anolis cuvieri*. They agree partly in having the scales of the back in places slightly separated from one another by the interpolating of more or less scattered, inconspicuous, and irregular small or minute granules, though these in no way encircle the scales. In general the scales of the back present an imbricated appearance. I have for these reasons allowed the species to stand near *Anolis cuvieri*. Its differences are, however, slight, and as the young of *Anolis cuvieri* is unknown, I first thought it to be such, especially as all my examples are comparatively small. It would appear too great a latitude in variation to admit such characters as these specimens present as simply variations due to age. First is the contact of several pairs of the large scutes of the supraorbital semicircles, rarely separated by a single row of very small scales. Second, the occipital scale is distinct and usually large, though often separated by only one scale from the supraorbital semicircles. The labials are in contact with the infraorbital semicircle, a character constant in every specimen. In agreement with *Anolis cuvieri* are the rows of large scales between the rictus and the ear, which vary from 5 to 8. This character will

readily serve to distinguish it from the common *Anolis cristatellus*. The present new form presents a considerable resemblance to *Anolis monensis* Stejneger (known only from Mona Island) in the larger scales and rather uniform coloration, though it has small post-rictal scales like its near ally *Anolis cristatellus*.

Named for Dr. Alfred G. Mayer, of the Carnegie Institution of Washington.

**Anolis gundlachii Peters.**

Eight examples, the largest 176 mm. in total length, from a small settlement up the Rio Grande, 2 miles above Arecibo, Porto Rico, on June 12, 1915.

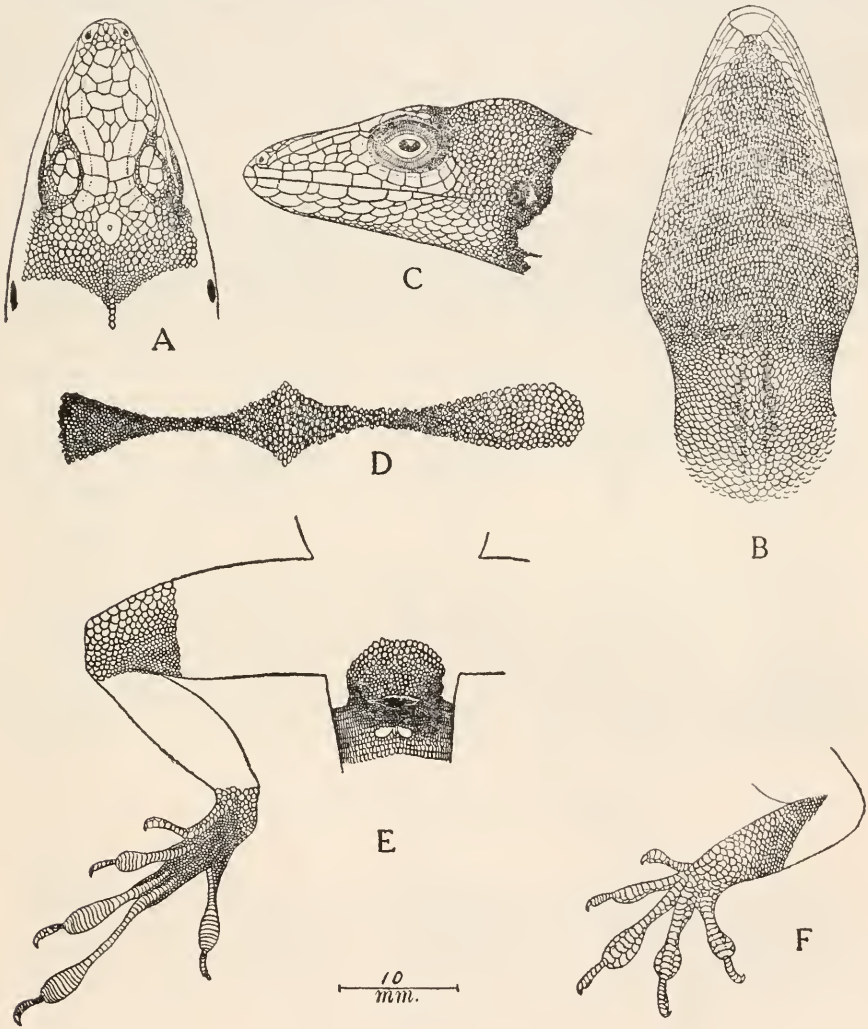



FIG. 4.—*Anolis mayeri* sp. nov.

A, upper surface of head.
B, lower surface of head.
C, side view of head.
D, transverse lepidosis of trunk.
E, lepidosis of hind toes, knee, and vent.
F, lepidosis of fore-arm and fingers.

Color in alcohol uniform dull brownish-olive generally above. Lips pale or whitish, labials obscurely dusted with sooty dots. From gape of mouth back, including ear, whitish band well defined and extending to groin. Immediately below this a gray-brown narrow area all along to groin, fading out in pale color of lower surface, which is largely whitish. Nearly all examples show belly with very pale blue-green tinge. Dewlap yellow-ocher. Some examples are more grayish than others and most show fine specks or dots of dusky on the side above and the costal region below pale lateral streak. The contrasted and bright markings noticed by Dr. Stejneger in living examples are not evident in these preserved specimens. Dark cross-blotches are, however, seen obscurely, though in smaller examples they are far more noticeable. Scales of the supraocular semicircles usually separated by one row of scales at least, often two rows present, and sometimes partly in contact.

Besides the above, 6 examples were obtained from Utuado. These often show but a single row of scales separating the supraocular semicircles.

**Anolis cristatellus Duméril and Bibron. Figure 5.**

A very large series, represented by nearly 300 specimens from various localities. A large series from Guanica, Porto Rico, shows usually the supraocular semicircles in contact, though the size and disposition of the plates present great irregularity. In color some are very finely vermiculated with darker lines. Often the upper surfaces of the limbs present an obscurely barred

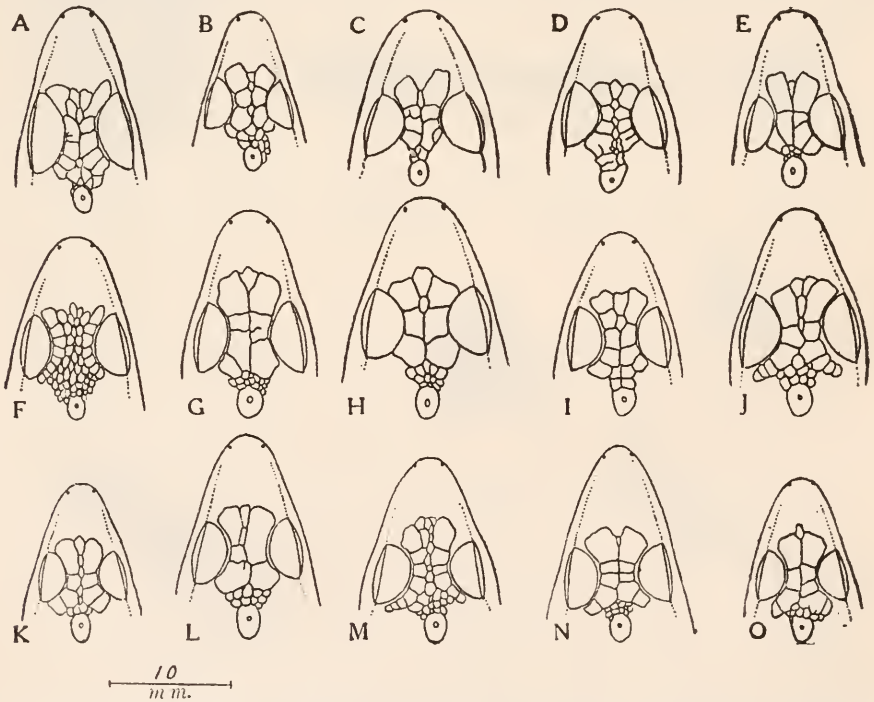



Fig. 5.—*Anolis cristatellus* Duméril and Bibron. Lepidosis of the supraocular semicircles. Figs. A to D and L and M from Guanica, E to H from Arecibo, I to K from Utuado, N and O from Virgin Islands.

appearance, and in some cases they are finely vermiculated. Many examples are more or less olivaceous. In a small series from Guanica one example shows a quite distinct whitish vertebral stripe. Several are pale or light gray.

A large series from Utuado, collected both in the town and down the Arecibo River, June 12, are very variable, both in color and squamation of the head. In color these examples appear much more mottled than others. The chin and throat are variable, and may be streaked or uniform, especially in small or young examples. Some show a considerably developed nuchal crest. Often the labials may be marked with dark blotches, giving the lips a cross-barred appearance. Some examples show five or six obscure dusky or blackish saddles on the back. Occasionally a pale vertebral band is seen down the back. Though the squamation of the head is quite variable, usually the supraocular semicircles have two pairs of plates in contact, often one or two small ones may be interpolated in the median line, and occasionally a median series of small scales (in one instance double) entirely separates them. The largest of this series is 175 mm. in total length.

Thirteen examples obtained at a small settlement up the Rio Grande, 2 miles from Arecibo, on June 14, 1915. Several show a pale vertebral streak on the back and a longitudinal blackish streak along each side of the back, mostly with narrow pale bordering line. Sides of body may also present obscure irregular dark blotches forming smaller spots or speckled appearance below. In some, the lower surface of the body is yellowish in alcohol.

Two from the Arecibo River near the 70-kilometer post, June 14, 1915. One light gray, conspicuously mottled with darker, another with the pale vertebral band bordered each side with a blackish lengthwise band.

A large series from the Virgin Islands, many showing the white vertebral band on the trunk, occasionally interrupted. Many have the chin speckled. Frequently a dark spot occurs behind the occipital plate, sometimes divided to form one on each side.

**Anolis stratulus Cope.**

Four from Guanica, 2 from Utuado, 3 from a small settlement up the Rio Grande 2 miles from Arecibo, Porto Rico, and 3 from the Virgin Islands. Considerable variation in color is noticeable and a few show distinct dark saddles on the back. All are more or less finely speckled with darker color; in some cases the marbling gives quite a variegated pattern, due to the variable small or large dark spots. The Virgin Islands examples show the back marked with blackish transverse saddles. Dewlap bright yellow in alcoholic specimens.

Variation in the squamation is often seen. Some specimens show one or two pairs of plates of the supraorbital semicircles in contact.

**Anolis krugi Peters.**

Five examples from Guanica, Porto Rico, now show the dewlap red.

Ten from Utuado, on June 12, show the dewlap crimson in alcohol. Sides and lower surface largely brilliant yellow. In these examples the squamation of the supraocular semicircles is often quite variable. While they may be separated by one row of scales, or sometimes two rows, the rows are frequently incomplete, so that the supraoculars may be in contact with at least one of their pairs.

Five from the Arecibo River near the 70-kilometer post, on June 14. These all have but one row of scales between the supraocular semicircles.

**Anolis pulchellus Duméril and Bibron.**

Seven very interesting examples from the Virgin Islands which agree very well with Dr. Stejneger's description and figures of Porto Rican material. In alcohol these examples are all pale brownish. A dark brownish, well-defined streak alongside of snout below canthus rostralis to eye and continued back from latter well above ear alongside of back, and on trunk more or less broken into spots irregularly to groin. Below ear on each side of lower surface of head a brownish streak to shoulder, though not evident in young. Upper surface of body or back between dark lateral bands with speckling of brownish, mostly obscured, and arranged largely in lengthwise courses. Similar markings also seen on upper surface of head in some examples.

Variation is seen in the scales separating the supraocular semicircles. In one case a pair of plates of the latter are largely in contact, in another instance two rows of scales intervene, while in the other a single complete row occurs.

**Anolis poncensis Stejneger.**

Four from Guanica, Porto Rico. This species was heretofore known only from the type locality at Ponce, where it was obtained April 16, 1900. It differs from the other Porto Rican species of *Anolis* in the completely keeled scales of the back, sides, and belly. In coloration my material agrees with Dr. Stejneger's account, the young or smaller example showing the pale vertebral band bordered on each side by a dusky parallel and equally wide band. It also shows a pale obscure orange blotch at and on each side of the occiput, the whole three indistinctly joined. One example is conspicuously greenish above, mottled with dusky.

The squamation of the supraocular semicircles is sometimes quite irregular, and these may have two pairs in contact or be separated by a very narrow median row.

**TEIIDÆ.**

**Ameiva exul (Cope).**

Six from Utuado, Porto Rico, some showing the granules extending forward to the second chin-shield. In one an accessory scale is interpolated between the preparietals and in contact with the parietal.

One from the Arecibo River near the 70-kilometer post, on June 14.

One from a small settlement on the Rio Grande 2 miles from Arecibo, on June 14. It shows two very large plates on the inner tibial surfaces.

Among 13 examples from the Virgin Islands, one shows the prefrontals separated by a small accessory scale, and another has the same scale and frontal divided into three equal scales, two of which are in front as a pair; 3 more examples from the Virgin Islands show the occipital plates rounded and subequal; one also shows an additional plate bordering the third and fourth supralabials and interposed between the loreal, first subocular, and preocular.

**Ameiva wetmorei Stejneger. Frontispiece and Figure 6.**

*Description.*—Body elongate, rather slender. Tail long, conic. Head conic, muzzle long. Eyelids granular. Teeth rather large, conic, in one row, and becoming larger as they progress backward. Interorbital level. Ear about size of eye, and tympanum not deep. Hind foot about two-thirds combined length of head and trunk.

Front nasal plates meet rather narrowly in contact on top of snout. Nostril in suture between two nasals. Supraocular plates three, in contact with prefrontal, frontal, fronto-parietal, and parietal. Fronto-parietals united as a single plate before 3 large parietals, of which median is much narrowest. Suboculars narrow, first two each half length of last. Loreal in contact

with second and third labials, first three suboculars, first supra-preocular, prefrontal, fronto-nasal, and hind nasal. First supraocular in contact with first superciliary, loreal, prefrontal, frontal, and second supraocular. Second and third supraoculars separated from superciliaries by a narrow series of very small scales. Second supraocular in contact with first supraocular, frontal, fronto-parietal, and third supraocular. Third supraocular in contact with second, fronto-parietal, and parietal. Superciliaries of five plates, last small, about equal and all combined only equal in length to anterior one. A row of narrow occipital plates. Six superior and 5 inferior labials to rictus. Ear-opening not denticulated. First pair of chin-shields in contact, second pair separated only in front by narrow single row of small granules. Three rows of scales on gular fold, front and hind rows of about equal width, median row larger. Scales on upper surface of body and limbs minute. Brachium with one series of very broad plates externally and a narrower inner series. Antebrachium with three series of small plates. On under surface of tibia two rows of enlarged plates, outer row of much larger plates, and one above enormously enlarged. Eight rows of abdominal plates. Three large anals, one in front and two behind. Tail covered with rings of smooth scales.

Color in alcohol largely black above, with 7 longitudinal sharply defined narrow lines of very pale blue-green, distributed as follows: Median, much broader than the others, extends from tip of snout to tail, where it broadens

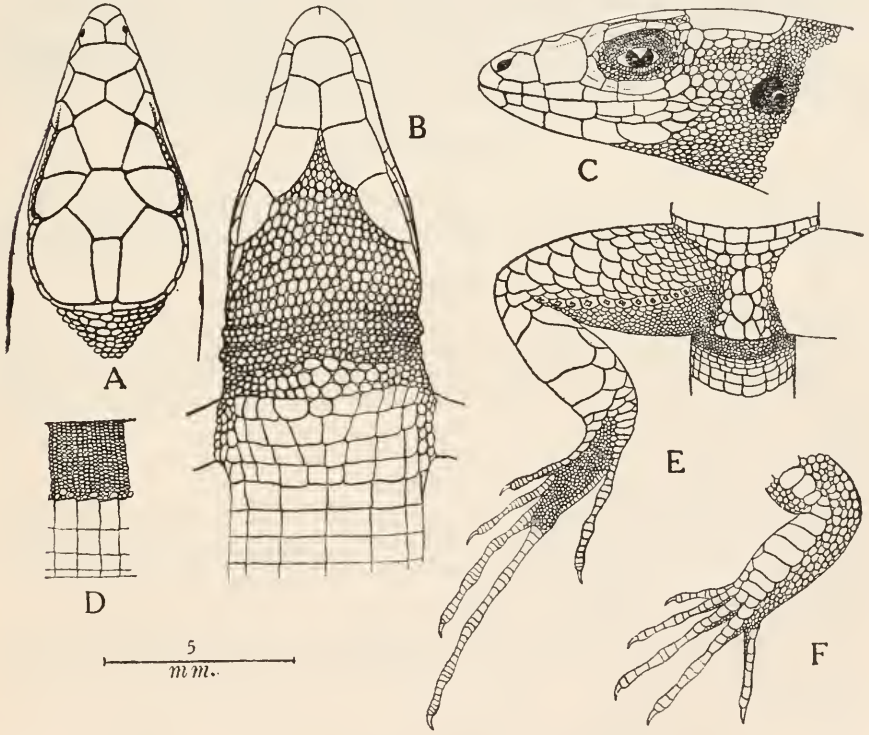



FIG. 6.—*Ameiva wetmorei* Stejneger.

A, upper surface of head.
B, lower surface of head.
C, side view of head.
D, transverse lepidosis of trunk in lateral view.
E, lepidosis of hind limb and ventral region.
F, lepidosis of fore-arm and fingers.

out and, like the others, fades in the more bluish color of the tail. A second streak includes the superciliaries and extends back on upper side of head till above shoulder. On each side, from lower edge of eye back over ear, along its upper edge, a narrow pale blue-green line extends back alongside of tail, fading out behind. Another similar line is on each side from lower ear-edge above shoulder back to groin; below this another still narrower line of same color from axillary to groin. Behind hind leg a single pale blue-green line extends back alongside of tail, fading out behind and much wider than lines ending in groin. Upper surface of limbs blackish like back, each forearm with lengthwise median pale blue-green line, broken in one or more places, and continued up on upper arm as several spots. Several pale spots on outer surfaces of limb in black field. Upper surfaces of hind limb conspicuously spotted with pale blue-green. Under surface of body mostly uniform pale blue-green. Feet and hands dark above, pale below. Tail largely pale bluish, especially terminally.

Color in life with tail greenish-blue (coppery-blue), ground-color above black and below pinkish gray. Dorsal median longitudinal stripe, and three lateral longitudinal stripes, deep straw-yellow. Shorter stripes begin at both nostrils and extend to groin. Legs spotted yellow on brownish-black ground-color.

Total length 103 mm., from snout tip to vent 31 mm.

One example from Ensenada, Porto Rico, June 1, 1915. Collected by Mr. M. H. Sanborn.

The above is the only example I have seen, though several others have been reported. Its striking coloration will at once distinguish it from the well-known *Ameiva exul*. Apparently not reported since described.[1]

### AMPHISBÆNIDÆ.

**Amphisbæna cæca Cuvier.**

One from Guanica. Rings on body 217, on tail 17. Long occipitals more than half length of frontals. Length 130 mm. Collected by Mr. M. H. Sanborn.

### BOIDÆ.

**Epicrates inornatus (Reinhardt).**

One from Guanica, collected by Mr. Sanborn. Ventrals 264, subcaudals 75. Indistinct blotches are seen all along the body, numerous and most distinct on hind part of body and tail. Ventrals largely uniform deep dusky brown. Length 1,675 mm.

### CORONELLIDÆ.

**Leimadophis stahli Stejneger.**

Two from Guanica, besides one obtained on a coffee plantation in the mountains 5 miles west of Utuado. They show ventrals 154 to 157, subcaudals 90 to 92, anals 2, scales transversely on back 19. Length 363 to 382 mm.

**Alsophis portoricensis Reinhardt and Lütken.**

Two from Guanica, collected by Mr. Sanborn. Ventrals 172 to 180, subcaudals 116 to 118, anals 2, scales transversely over back 17. Length 534 to 1,057 mm.

**Alsophis antillensis (Schlegel).**

Five from the Virgin Islands. They show ventrals 172 to 183, subcaudals 124 to 130, anals 2, scales transversely over back 19. Length 368 to 943 mm.

[1]Proc. Biol. Soc. Washington, xxvi, 1913, pp. 69-72. Guanica.

**Alsophis rufiventris Duméril and Bibron.**

One from the Virgin Islands, from which the species has not been previously recorded. Ventrals 212, subcaudals 92, anals 2, scales transversely over back 23. Length 943 mm.

**EMYDIDÆ.**

**Pseudemys palustris (Gmelin).**

A series of 10 very interesting examples from Guanica Lake, Porto Rico. On first examination they appeared to represent two distinct species, and it appears that two very great extremes of color variation occur in Porto Rico. Dr. Stejneger pointed out in 1902 that "there are indications at hand that there may be some constant differences between those inhabiting the different islands, but the material at my disposal is not sufficient to warrant an attempt to separate them."

Later Dr. Barbour says: "There are specimens at hand from Jamaica (type locality), Cuba, Haiti, and Porto Rico. They do not, however, vary in such a way as to warrant the designation of varieties confined to each island. Stejneger and I (Bull. M. C. Z., 1910, 52, p. 301) had both expected that such subspecies might be defined. As yet, however, the material available for study is very meager. The species is very shy, and is usually confined to lowland muddy pools."

Thus, as little appears to be known concerning this species, a few notes on the variation are given below. All my examples were secured in the lowland lake at Guanica. Dr. Stejneger's figures 185 and 186 represent what may be considered typical (in a restricted sense) of *palustris*. This shows specimens which have the pale lengthwise lines on the sides and lower surface of the head. In this form the carapace is more of a uniform color, without dark blotches or spots, and the plastron may be marked with dark lines along the sutures of the plates, which may vary to very obsolete or even be wanting. About 7 of my examples, representing both sexes of this form, are in the collection.

The remaining three specimens exhibit a different pattern of coloration. They also differ in having the front claws a little longer than the longest of the preceding. The carapace in all is decidedly paler over and about the anterior third than the rest of its extent, showing but few markings, and these now obscure, though the sutures of all the plates are conspicuously blackish. The sutures of the plastron and all the lower marginal plates of the carapace are also marked with blackish. The carapace is also largely speckled or blotched with darker. The color-pattern of the head is strikingly different from the other specimens and is shown everywhere with narrow blackish wavy or vermiculated lines, often broken or irregular. The feet are similar.

The latter variety was first noticed by Gray as *Emys vermiculata*,[1] and the type locality given as tropical America. I have not seen his subsequent plate,[2] though under *Trachemys rugosa* he gives[3] the following description of "*Emys vermiculata* Gray": "Shell 7⅓ in. Back brown, closely black-dotted; sternum and under side of margin very closely spotted. Sternal shields dark edged." The locality is given as the West Indies. Sowerby and Lear figure the *Emys rugosa*,[4] a fairly good representation of the present variety.

The interesting figure by Cocteau[5] agrees with the above in the speckled carapace and dark-edged sutures of the plastron. The head is streaked as in the examples here allowed as typical *palustris*.

[1]Cat. Tort. Brit. Mus., 1844, p. 25.
[2]Cat. Shield Rep. Brit. Mus., 1855, plate 13.
[3]Hand-List Shield Rept. Brit. Mus., 1876, p. 46.
[4]Tort. Terrap. Turt., 1872, plates 42, 43.
[5]Hist. Nat. Cuba, Sagra, Rept., 1844, plate 2.

A. HOEN & CO. LITH.

Ameiva wetmorei Stejneger. Enlarged about three times.

II.

# FISHES NEW TO THE FAUNA OF PORTO RICO, WITH DESCRIPTIONS OF EIGHT NEW SPECIES.

By CHARLES F. SILVESTER,

Curator of the Zoological Museum of Princeton University.

Four plates.

# FISHES NEW TO THE FAUNA OF PORTO RICO, WITH DESCRIPTIONS OF EIGHT NEW SPECIES.

By Charles F. Silvester.

Little more than half of the known species of West Indian fishes have been recorded from Porto Rico. Since the work of Evermann and Marsh,[1] Nichols[2] has added 22 species to the fauna of the island. Two of these were new to science.

In May and June 1915, the writer spent three weeks on the island as a member of an expedition to Porto Rico under the auspices of the Carnegie Institution of Washington. The results of this work are to be incorporated with a more extensive investigation of the fishes of the island, but it seems best at this time to publish, at least, descriptions of the new species.

It is with pleasure that the writer acknowledges his indebtedness to Dr. Henry W. Fowler for much valuable assistance and supervision in working up the collections. Through the courtesy of the Academy of Natural Sciences of Philadelphia comparisons have been made with specimens in their collections.

## MORINGUIDÆ.

**Aphthalmichthys mayeri sp. nov. Plate 1.**

Head 9.2 in body; 4.2 in tail; 13.4 in total length. Depth same as upper jaw, 5 in length of head, about 65 in total length; snout 7 in head. Lower jaw projecting; anterior nostril tube-like, near end of snout; posterior nostril larger, in front of eye. Teeth retrorse; eye small but not rudimentary. Interorbital space two-thirds length of snout. Vertebræ 74+46. Spinous processes prominent anteriorly; transverse processes large throughout. Gill-opening one-half the isthmus, which is the same as snout. Gape not as wide as in *A. caribbeus*. All the fins very rudimentary, microscopic, excepting caudal; pectoral less than one-half width of gill-opening; dorsal and anal begin length of head behind vent and continue as very fine lines to end of tail, where they enlarge into the easily visible caudal. Lateral line present and prominent, with series of microscopic, open pores; blood-vessel follows course of and shows through skin on lateral line.

Color in life orange-yellow above; ventral surface slate-blue, merging into whitish in anterior part of tail region; posterior part of tail entirely yellow; iris blue. Tip of lower jaw and area behind eye reddish, fading to pale flesh-color in spirits. Color in *A. caribbeus* much darker in spirit preparations.

In a preliminary list of "Fishes New to the Fauna of Porto Rico," published in Year Book 14 of the Carnegie Institution of Washington, the writer was in error in placing this species in the family Murænesocidæ and in making it the subject of a new genus. As Gill and Smith have shown (Science, n. s., vol. xi, No. 286), the genus *Stilbiscus* is identical with the genus *Moringua* and

[1]Aquatic Resources and Fisheries of Porto Rico, U. S. Fish Commission Bulletin for 1900.
[2]Bulletin of the American Museum of Natural History, vol. xxxiv, article vii, pp. 141–146.

must be referred to the family Moringuidæ. This family up to that time had not been known to be represented in American waters.

A careful comparison has been made with a specimen of *A. caribbeus* collected at San Juan by Professor Conklin. These two species are very closely related, but *A. mayeri* may be distinguished at once by its striking color. The type was kept alive for more than two weeks in an aquarium at Guanica and during this period no color changes could be noted; in spirits *A. caribbeus* is much darker in color; microscopic examination shows many more chromatophores. The grooves for the dorsal and anal fins, so well marked in *A. caribbeus*, are very little evident in *A. mayeri*.

Two specimens of this beautiful little eel were obtained on the sand flats around mangrove swamp west of Guanica Harbor at very low tide.

Type, No. 3073, Zoological Museum, Princeton University; 310 mm. long.

Paratype, No. 3126, Zoological Museum, Princeton University; 28 cm. long.

Named for Dr. Alfred G. Mayer, director of the expedition.

### MYROPHIS.

**Myrophis longleii sp. nov. Plate 2, fig. 1.**

Head 3.5 in trunk, 5.7 in tail. Depth of body at gill-opening 3.3 in head. Upper jaw projecting; teeth sharp, more or less irregular on maxilla and vomer, indicating two series; series more or less single on mandible. Eyes rather high. Interorbital space 1.5 times eye. Snout broad. Eye 1.5 in breadth of snout between anterior nostrils, 2.5 in snout. Tail compressed. Body slightly compressed. Greatest width of head greater than body behind gill-opening. Vertebræ, abdominal 53, caudal about 100. Ribs developed. No neural spines. Vertical fins well developed; dorsal beginning two-thirds length of head in front of vent, anal beginning directly behind vent; both continuous into caudal, which is wider and completely surrounds end of tail. Anterior nostril tube-like, near end of snout; large pore above this on top of snout. Posterior nostril in upper lip.

Color in life, light olive-green with very fine punctation above, lighter below.

Type, No. 3083, Zoological Museum, Princeton University. Length, 12 cm.

Dug from sand flats west of Guanica Harbor.

Named for Dr. W. H. Longley.

### OPHICHTHYIDÆ.

**Myrichthys kecki sp. nov. Plate 2, fig. 2.**

Head 4 in trunk, 9.5 in total length; eye 3 in snout, snout 4.6 in head. Teeth more or less blunt in single series; vomerine teeth present. Pectoral small, as wide as gill-opening, but very short and rudimentary. Isthmus about 3 times width of gill-opening. Numerous pores on top of head and on lower jaw; large round pore on center of opercle. Anterior nostril near end of snout in large tube which projects downward. Posterior nostril under eye in lip. Dorsal well developed, begins on nape and extends to near tip of tail; anal very low, beginning directly behind vent and extending to near tip of tail. Tail projecting very little beyond dorsal and anal. Branchial chamber rather large.

Color in life light transparent brownish-green, darker above, series of about 20 clusters of darker spots along lateral line, hardly distinguishable in life. This specimen shows different color-markings from other members of this genus, but is no doubt a young specimen and therefore little importance can be laid on the color, which is so subject to change with the growth of the individual. The relative measurements and proportions warrant classifying it as a new species.

One specimen, dug from mud flats near mangrove island west of Guanica Harbor. Length, 7 cm.

Type, No. 3082, Zoological Museum, Princeton University.

Named for Mr. Thomas Keck.

### BELONIDÆ.

**Tylosurus notatus (Poey).**

One specimen, 26 cm. long, seined among mangrove islands west of Guanica Harbor.

No. 3121, Zoological Museum, Princeton University.

### SYNGNATHIDÆ.

**Corythroichthys ensenadæ sp. nov. Plate 2, fig. 3.**

Rings 18+33; dorsal 19, on 1+4 rings; pectoral 12; caudal 10; anal 2. Head 9. Eye 5. Body 1.5 in tail. Cranial ridges strong, median keel on snout to middle of eye; ridge on occiput high, notched in front and behind. Supraocular ridge beginning in tubercle in front of center of eye; two ridges on opercle. Nostril double, in front of and near eye, tubed, dorsal tube short, ventral tube longer. Keels on body and tail strong; lateral keel of body running into ventral caudal keel. Belly convex, keel strong.

Body with 22 yellow and 22 brown bands, each covering from one to two body rings, some of which divide on the ventral surface of belly into rings and blotches of brown. Brown bands edged with darker. Bands on snout become irregular spots and blotches. First brown band crosses interorbital space through eye and obliquely downward and backward to large brown area on ventral surface of opercle.

Closely related to *C. albirostris*, but well defined in color-markings.

Vertebræ and body rings correspond.

Type, No. 3084, Zoological Museum, Princeton University. Length 10.5 cm.

From bunch of coral off Ballenas Point.

Named for a party of friends from Ensenada, who obtained this specimen.

### CHEILODIPTERIDÆ.

**Amia conklini sp. nov. Plate 3, fig. 1.**

Head 2.6; depth 2.7; eye 2.6; interorbital 3.2; dorsal VI–I, 9; anal II, 9; scales 2–27–7; eye large, 2.5 in head; head broad; mouth rather large. Lateral line complete, following curve of back to caudal peduncle, where it dips down to center line. Anterior nostril near front of snout; posterior nostril large oval opening in front of center of eye.

Color orange-red with clusters of small black specks bordering scales over entire body. Caudal peduncle with large oblong black spot; caudal edged with black; spinous dorsal black; soft dorsal and anal with black bar at base; a black bar extending downward and backward on front of preopercle from eye; another bar extending transversely on nape and down on opercle, where it is more or less broken up into series of dots.

Differs from *A. sellicauda* in color markings, larger eye, and more robust body. Examples of *A. sellicauda* were obtained on the same coral reef, and this species differs distinctly from *A. conklini*, the proportions and color markings being quite different. *A. conklini* does not fade to white in spirits and the clusters of minute dark dots bordering each scale do not fade.

Two specimens, 4.5 and 5 cm. long, obtained with dynamite on coral reef off Guanica Harbor.

Type, No. 3080, Zoological Museum, Princeton University. Length, 5 cm.

Paratype, No. 3128, Zoological Museum, Princeton University. 4.5 cm. long.

Named for Professor E. G. Conklin.

**Apogonichthys stellatus Cope.**

Three specimens, 1.5 to 2.5 cm. long. Inhabits dead sea-urchin shells. Almost every sea-urchin skeleton in small muddy area west of Guanica Harbor was inhabited by one of these delicate little fishes. The individual was never found more than a foot or two away from its shelter and when disturbed or approached darted into the shell. At low tide or when the surf was breaking over the mud flats the fish was invariably found inside the shell.

Measurements of the largest individual are as follows: Depth 3; head 2.7; eye 3; snout 5; scales 2–27–6. The chromatophores take the form of stellations in spirit preparations. In life this fish is a uniform dark brown, almost black, with no evidence of bars or spots.

No. 3048, Zoological Museum, Princeton University.

## CENTROPOMIDÆ.

**Centropomus pectinatus Poey.**

One specimen, about 20 cm. long, from Guanica Lake.

## SPARIDÆ.

**Diplodus argenteus (Cuvier and Valenciennes).**

From coral reef off Guanica Harbor.

## SCIÆNIDÆ.

**Eques pulcher Steindachner.**

One specimen, 5 cm. long, from cluster of coral rock in shallow water west of Guanica Harbor.

No. 3097, Zoological Museum, Princeton University.

## POMACENTRIDÆ.

**Microspathodon niveatus (Poey). Plate 4, fig. 1.**

Head 2.7; 3.4 in total length. Depth 1.7; 2.5 in total. Eye 2.5; snout 3. Dorsal XII, 15; anal II, 13. Scales 3–25+6–10. Mouth small; maxillary reaching to nostril. Upper teeth small, movable; lower teeth twice as large and more or less fixed.

Color in life uniform deep marine-blue with about 35 pure-white silvery spots, each the size of a scale, covering the entire body. More numerous on dorsal fin and dorsal part of head and body. When seen in the sunlight these spots reflect light and appear like so many points of fire.

Many specimens of this beautiful fish were seen swimming among the corals of the western end of Rajos de la Parda; they varied in length from about 2 to 4 inches. The color was the same in all. Only one specimen was obtained, 2.12 inches long, from which the above description was taken.

No. 3099, Zoological Museum, Princeton University.

**Microspathodon chrysurus (Cuvier and Valenciennes).**

Several specimens observed on the coral reefs off Guanica Harbor, but none were obtained.

**Microspathodon fowleri sp. nov. Plate 4, fig. 2.**

Head 3.2; depth 1.87. Dorsal XII, 15. Anal II, 13. Scales 3–29+7–10, 21 pores. Eye 3.9. Body compressed, but rounded; profile from snout to dorsal evenly rounded; slight indication of fleshy crest at nape in 1 individ-

ual, not indicated in 4 individuals. No fleshy corrugations on anterior profile in 4 individuals, indicated in 1 individual. Nostril small. A pigmented, fleshy, tongue-like flap in roof of mouth. Upper teeth small, movable, in semicircular series; teeth of lower jaw large and fixed, in a series rounded in front and concave on sides. Length of caudal peduncle about 2.5 in head, its depth 2.2 in head. Dorsal elevated and ending in a pointed tip behind. Color uniform deep-black to uniform bluish-black, with indication of yellowish tinge under scales; fins uniform black.

Type, No. 3060, Zoological Museum, Princeton University. Length, 19 cm.

Five individuals, 13 to 19 cm. long, from coral reef off Guanica Harbor.

Named for Henry W. Fowler, in recognition of his contributions to ichthyology.

### LABRIDÆ.

**Bodianus rufus (Linnæus).**

One specimen, about 15 cm. long, from coral reef off Guanica Harbor.

**Iridio maculipinna (Müller and Troschel).**

Common on the coral reefs off Guanica Harbor.

### MONACANTHIDÆ.

**Pseudomonacanthus amphioxys (Cope).**

Three specimens from coral reef off Ballenas Point.

### GOBIIDÆ.

**Sicydium antillarum Ogilvie-Grant.**

Several specimens, 5 to 12 cm. long, obtained from mountain streams flowing into the Arecibo River in the vicinity of Utuado. Only one specimen corresponds to the description of the type; 12 other specimens of this genus were obtained; these vary enough to indicate 6 different species. However, careful comparisons would indicate that much of this variation is individual and not specific. For example, microscopic examinations indicate that the filamentous character of the spinous dorsal is sexual and not specific. Two male specimens of what appeared to be *S. caguitæ* had the dorsal filaments, while three females did not possess this character. The scales in the 12 individuals varied from 53 to 84. Young individuals show fewer scales than older ones.

Color in life varied from almost pure white to blue black. Mr. M. H. Sanborn invited my attention to examples of this genus which were almost pure white, found in small mountain streams flowing from caves. Several specimens of this beautiful little fish, 2 to 3 inches in length, were observed by the writer and one specimen was obtained. Observations would indicate that this is a breeding female of possibly a new species. The morphological characters, however, do not warrant making a new species until other individuals of both sexes can be obtained, as well as specimens taken at different seasons of the year.

Several individuals showing the color markings of *S. plumieri* were obtained. They do not show the emarginate caudal nor the large number of scales. They are probably the young of *S. antillarum.*

The writer is of the opinion that *S. vincente* Jordan and Evermann is the young of *S. plumieri* (Bloch).

The fin rays and the vertebræ were constant in all specimens.

Dorsal VII, 11. Anal 11. Vertebræ 26 = 10 + 16.

**Gobiosoma viridistriatum sp. nov. Plate 3, fig. 3.**

*Gobius lineatus* Poey, Mem., II, 424, 1861, Cuba. Preoccupied by *Gobius lineatus* Jenyns.

Head 3.4 to base of caudal, 4.2 in total length; depth 5 in total length. Dorsal VII–I, 11; anal 10; ventral 6. Snout same as eye; eye 4 in head; interorbital space about 3.5 in head. Gills 4; pseudobranch present. Nostrils double, well separated. Anterior nostril in tube above upper lip; posterior in very short tube in front of upper third of eye; upper lip large. Branchiostegals 3. Vertebræ 11+16? A few large open pores on head, large one behind eye. A series of very minute barbel-like organs following course of under jaw extending back to ventral surface of opercle.

Body with 20 well-defined vertical brilliant green bars, edged with darker, and separated by 21 narrower yellowish-white bars. A brilliant red band extends from tip of snout through eye to above gill-opening. Bars and bands fade to brown and white in spirits.

Obtained from branches of dead coral east of entrance to Guanica Harbor.

Type, No. 3079, Zoological Museum, Princeton University. Length, 23 mm.

Paratype, 19 mm., No. 3126, Zoological Museum, Princeton University.

This is undoubtedly the species described by Poey under the name of *Gobius lineatus*, from Cuba. It is quite distinct from *Gobiosoma multifasciatum* of Steindachner and for this reason is here described and named.

## GOBIESOCIDÆ.

**Gobiesox cerasinus Cope.**

Quite common around coral reefs in vicinity of Guanica Harbor. Usually hidden in crevices of rocks.

## BLENNIIDÆ.

**Alticus macclurei sp. nov. Plate 3, fig. 2.**

Head 4.2; depth 4.3. Dorsal XII, 20; anal 23. Head slightly longer than deep; anterior profile vertical, slightly concave. Eye 3.25 in head. Pectorals reach to vent or beyond in male, not quite to vent in female. Ventrals 1.5 in head. Upper lip of male large; teeth pectinate; canines large; fringe around upper and lower lips; upper lip pigmented, lower not pigmented in spirit specimens, yellow in life. Supraocular tentacles slender; large tentacle medial to each anterior nostril, which divides into 5 or 6 tentacles; two nuchal tentacles in male, smaller in female. Numerous large pores on head, one group behind and below eye, another on supraopercular region. Dorsal fin entire, extending from nape to caudal; last dorsal ray bound down for two-thirds of its length; last anal ray free. Last dorsal and last anal rays small; do not show except in radiograph.

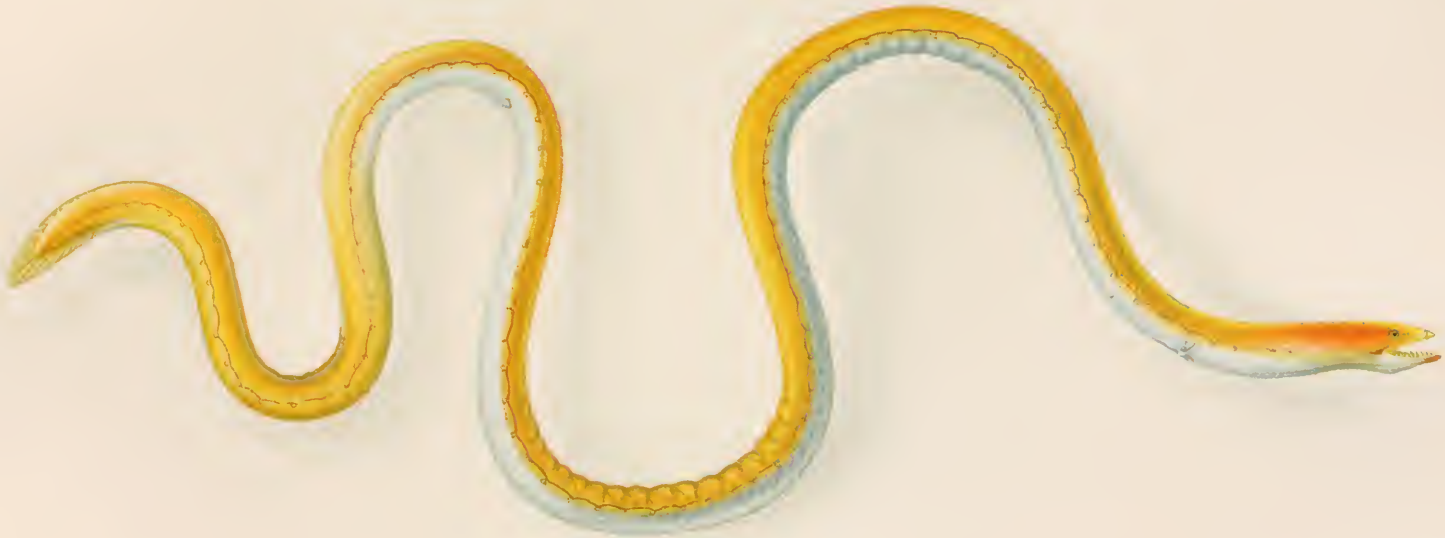
Differs generally from *A. atlanticus* in coloration. General color brownish, livid purplish on costal region; filaments above eyes and edges of lips bright orange. Iris slaty. Dorsal olive-greenish with median dusky lengthwise band anteriorly, contrasting strongly with whitish or pale upper half of fin, but sloping up behind so that edge of dorsal is dusky posteriorly. Upper front edge of dorsal broadly orange below, with submarginal area of whitish. Caudal olivaceous, dusky medially, grayish below, yellowish above; anal dark neutral tint, edge blackish; pectoral pale orange, red on lower half; ventral pale. Vertebræ 12+22.

Two specimens from dead coral reef west of Guanica Harbor.

Type, No. 3081, Zoological Museum, Princeton University; 5.5 cm. long.

Paratype, No. 3027, Zoological Museum, Princeton University; 5 cm. long.

Named for Professor C. F. W. McClure, for his researches upon the lymphatics of fishes.



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Aphthalmichthys mayeri Silvester. Type.

1

Myrophis longleii Silvester. Type.

2

Myrichthys kecki Silvester. Type.

3

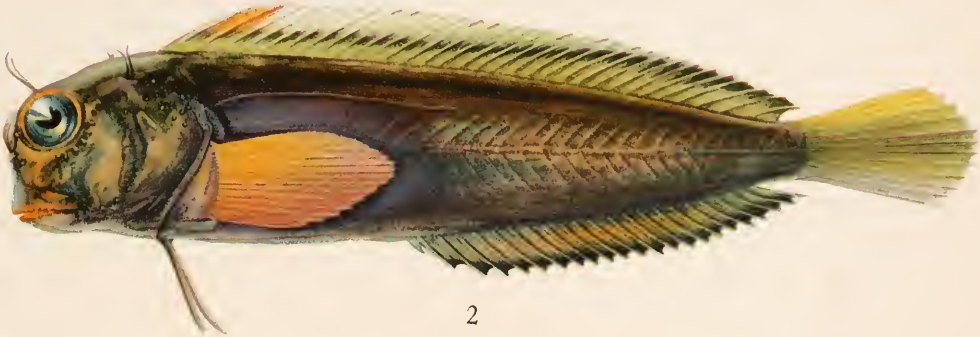
Corythroichthys ensenadae Silvester. Type.



A. HOEN & CO. LITH.

1

Amia conklini Silvester. Type.



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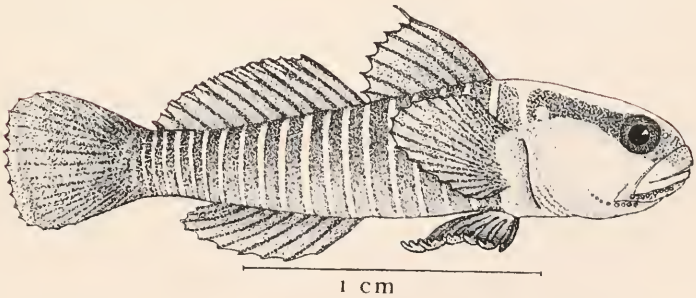
Alticus macclurei Silvester. Type.




3

Gobiosoma viridistriatum Silvester. Type.

A. HOEN & CO. LITH.

1

Microspathodon niveatus (Poey).

2

Microspathodon fowleri Silvester. Type.

A. HOEN & CO. LITH.

III.

# ORAL GESTATION IN THE GAFF-TOPSAIL CATFISH, FELICHTHYS FELIS.

By E. W. GUDGER,

Professor of Biology in the State Normal College, Greensboro, North Carolina.

Four plates.

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# ORAL GESTATION IN THE GAFF-TOPSAIL CATFISH, FELICHTHYS FELIS.

By E. W. Gudger.

## INTRODUCTION.

In a previous paper (Gudger, 1916) I have given in some detail the story of how I came to rediscover the habit of oral gestation in the gaff-topsail catfish, *Felichthys felis* (plate 1, figure 1). In order to give the facts contained in this paper their proper setting, a brief résumé of the data contained in the previous article will here be set forth.

## NARRATIVE.

In the summer of 1906, while at Cape Hatteras, North Carolina, Mr. N. F. Jennett, who operated a pound-net fishery in Pamlico Sound at that place, told me that in looking over the catch of his net on the previous day he had found a number of flat-whiskered ocean catfish, and that in handling these he had found in his hands a number of young. However, he was unable to say whether these had come from the mouth or the vent. At that time I was working in the Beaufort Station of the United States Bureau of Fisheries engaged in research on the embryology and breeding habits of fishes, so on my return I at once began to look up the literature as to habits of catfishes. I found that while there was a considerable literature on oral gestation in catfishes, certain rather definite conclusions were held that the smaller ocean catfish (*Galeichthys milberti*), also found at Beaufort and well known to me, is ovo-viviparous. Further, dissection of female gaff-topsails showed that the hinder part of each ovary, and especially the duct leading therefrom, was laid in plicated folds highly vascularized, in which it seemed possible for eggs to be held and nourished until hatched. However, on talking the matter over with a number of well-informed fishermen of Beaufort, I found that it was well known that the gaff-topsail carries in its mouth its eggs and even the larvæ after hatching. One man put it that he "had seen the sea-cat spit its eggs out of its mouth." Unfortunately the breeding season was past and it was impossible to investigate these conflicting reports by study of the fish; so it was necessary to let the matter stand over until the next summer.

At the beginning of the season at Beaufort in 1907, difficulties were had in collecting early material and in finishing my observations on the breeding habits and embryology of another fish; hence it was not until June 22 that it was found possible to make a trip for catfish. In the Narrows of Newport River, at Rockfish Rock hauling-ground,

a big catch of *Felichthys* was made. Thirty-two males carrying eggs were measured, and probably as many more were relieved of their oral burdens. Some half dozen of these were dissected and without exception all were found to be males. A large number of eggs was obtained, estimated at between 200 and 300, the greatest number taken from one fish being 26. These eggs were held loosely in the mouth, which was enlarged by a distension downward of the hyoid region and outward of the branchial arches, as shown in figures 2 and 3, plate I. Some of these eggs are shown in figure 8, plate III. Figure 7, plate III, is a photograph of the mouth of one of these fish with the eggs *in situ*. Attention is called to the extraordinarily distended mouth and to the great size of the eggs. One of these has two embryos.

Other trips were made during the summer of 1907, and scores of fish and hundreds of eggs were taken. Many observations and measurements of the adults were made; and much study was given to the eggs and larvæ, which were kept alive with considerable difficulty in aquaria in the laboratory. The result of all this work was the definite establishment of the fact that the male of the gaff-topsail catfish takes the recently spawned and fertilized eggs into his mouth and there nurses them until they are hatched and until the young are able to care for themselves.

During the summers of 1908, 1909, 1910, 1911 and 1912, the search for gaff-topsails was assiduously continued and no effort was spared to capture breeding males in the hope that early stages in the development of the eggs might be obtained. These efforts were attended by few successes and many failures. The failures in the seasons of 1908 and 1912 are mainly to be attributed to unprecedentedly heavy rainfall in the Beaufort region towards the close of May. These rains so freshened the water at the head of Newport estuary as to drive the catfish into the lower and broad stretches of the river, where it was found impossible to take them (despite almost daily seinings) at localities previously favored by the fish.

However, all the failures do not have so simple an explanation, for the fishermen, taking all possible precautions, made haul after haul in "holes" where recently or in previous seasons we had made fine catches, but the net came in with no catfish or at best with a few females or non-breeding males. In 1911, I even went so far as to make two trips to Beaufort; the first covering the time from May 13 to 18, the second for the season beginning May 25. The first time I was too early, the breeding not having commenced; the second time too late, the eggs having been laid during the interim.

These various failures were all the more regrettable because in the summers of 1908 and 1910, thanks to a grant from the Carnegie Institution of Washington, an artist was at hand to make drawings[1] for

[1]The drawings reproduced in this paper in figures 1, 2 and 3, plate I; and 9, 10, 11, 12 in plate IV, were made by Mr. E. A. Morrison under this grant.

the embryology of the fish. However, the work went on, and gradually the series of eggs was pushed both forward and backward until now there is a complete series illustrated by photographs or drawings from invagination to the adult embryo.

## HISTORICAL ACCOUNT.

The brief historical account herein contained will be confined to the gaff-topsail.

The first scientific man who seems to have had knowledge of this curious habit of the gaff-topsail was S. C. Clarke. In the *American Angler* for December 15, 1883, he says of the gaff-topsail in Florida: "The eggs of this species are golden yellow, and of the size of grapes, which they much resemble, in bunches of ten or twelve. The fishermen say that this catfish carries its young, when hatched, in its mouth." The following year this statement was republished in "Fishes of the East Atlantic Coast" by Van Doren and Clarke.

In 1883, and again in 1887, John A. Ryder makes brief mention of the fact that male catfish of the genus *Aelurichthys* (an old synonym for *Felichthys*) carry the large eggs (0.75 to 0.875 inch in diameter) in the hinder part of their mouth-cavities until the young are hatched. Unfortunately he gives no clue to the locality from which the eggs in his possession came.

Last of all comes Holder's (1904) brief mention of this habit in his delightful book of fishing stories entitled "The Boy Anglers." On page 175 is the following interesting statement:

> "Tom . . . secured . . . a gaff-topsail catfish . . . . As the boatman attempted to unhook it, he showed the boys its eggs packed on the inside of its mouth, where they are carried until they hatch; and even the young fish are protected in this way until they can care for themselves."

In 1908 I read a paper on this habit of this fish before the North Carolina Academy of Science, but not being ready to give out my observations, the title only was reported in the proceedings. In 1912, in the Proceedings of the American Association for the Advancement of Science for 1911, Section F, I published a short abstract giving the essential facts as to this habit, size of mouth-cavity, size, number of eggs, etc. Later I published the 1916 paper.

There is now to be given an account about which there is some doubt, but it seems best to insert it. Bloch (1794) figures (plate 365) a catfish from American waters which he calls *Silurus bagre*. This fish the Eigenmanns (1890) identify with *Felichthys felis*. In a former paper (Gudger, 1916) the question of identity has been discussed and there seems to be little reason to doubt that this identification is correct However, the point of interest just here is that on this same plate (365) Bloch has figured a little catfish sitting on a large yolk with its

tail bent upward at a sharp angle, but without anywhere referring to it, though in the adjacent text he has been discussing oral gestation in *Silurus militaris,* which he figures without barbels. However, some seven years after Bloch's death, Schneider, in editing the *Systema Ichthyologiæ* (1801) of his predecessor, says in a footnote to *Silurus bagre* (p. 378): "I have observed the eggs of this fish about to be hatched in the mouth." The larval form as figured by Bloch on plate 365 has 6 barbels and lacks the filament to the dorsal fin. Whether these are errors chargeable to the artist can not, of course, be determined. Possibly this little fish is the young of some other siluroid described by Bloch in the context. At any rate it may be noted here that Bloch is the first to describe oral gestation in siluroid fishes. The whole matter is very obscure, but the data are given here that the reader may draw his own conclusions. It is interesting, however, to note that, immediately after bursting the tough eggshell, the little gaff-topsail has the same high-waving tail as that figured by Bloch. (See fig. 10, plate IV.)

## THE BREEDING SEASON.

The limits for egg-laying by the gaff-topsail at Beaufort can not be set very narrowly, but an attempt will be made to indicate when males with eggs may be taken. This research was initiated the first week in August 1906, but only females long spent were taken. The real search for the fish was begun in 1907, when the first female was captured on June 4. Her ovary had in it no eggs over 10 mm. in diameter, but did show a lot of recently evacuated follicles. On June 6, other females were brought in having ova as large as 20 mm. Plainly, the breeding season was not over.

As explained before, it was found impracticable to search for the breeding males in 1907 until June 22, and the eggs taken on this day had on them young in various stages, but the majority had the whole yolk covered with the blood vascular system.

The search for early stages of the eggs began in 1908 on June 3. On this day a female with empty follicles was taken, as were others two days later. Notwithstanding daily seinings, no eggs were taken until June 11, and constant inquiries brought no news of the finding of a single egg by any of the fishermen before this date. Our failures, as explained elsewhere, were due to the freshening of Newport River by heavy rains. The youngest of these eggs had the yolk circulation covering quite half of the egg and were at least 10 days, probably 2 weeks old.

In 1909, the first eggs were taken May 27. These had on them forming embryos with a huge open blastopore behind. They were probably from 5 to 7 days old. However, a number of females were taken having enormous bellies due to the greatly swollen undischarged

ovaries. A number of these females were brought to the laboratory in a live-car and kept in the turtle pound. Four days later the largest of these was spawned artificially and gave up 68 grown eggs.

In 1910, the first eggs were taken May 21, before my arrival. These were few in number and low in vitality, whether because they were naturally infertile or because they had not been fertilized could not be determined. On May 25 we were fortunate in getting males with eggs in early invagination stages. These were probably 3 to 5 days old. On the following day more eggs of about the same stage were taken.

In 1911, as noted elsewhere, two trips were made to Beaufort for gaff-topsails. Having always been too late for early stages heretofore, I went too soon this year. The first seining was done May 13 and 40 or 50 huge females were taken, but from none of them could eggs be obtained. A large number of males was also caught but not one had the depressed hyoid region indicative of the breeding season. On May 15 a number of large females were obtained but none would give up eggs. The males, however, of this day's catch had enlarged oral cavities ready to receive eggs. None of these females had genital orifices markedly reddened. This spring was a late cold one and had evidently delayed the spawning beyond the normal time.

My second trip in 1911 gave me a seining on May 25. From this were obtained the youngest eggs ever gotten in this research—eggs with the invaginating edge of the blastoderm placed equatorially. Here again I was too late for segmentation stages, the eggs having been laid in my absence. However, they could hardly have been more than 3 days old.

The breeding season is plainly determined by the stage of ripeness of the eggs and this is pretty definitely fixed by the temperature. With a warm spring, egg-laying comes earlier, with a cold one later; but the evidence seems to be that once the laying begins it is quickly concluded. Normally this breeding season, as indicated by the data above given, begins about May 18–20, and rarely extends over 10 days, probably being concluded in even less time. This is plainly evidenced by the difficulty in finding early stages, and further by the fact that the majority of eggs taken in any season at any time are all about the same stage.

There must now, however, be given some data which contrasts markedly with the foregoing. On July 21, 1910, there were brought to me, by fishermen in Newport River, 2 male catfish with eggs and larvæ in their mouths. The 5 larvæ had their yolk-sacs four-fifths closed over by the body-walls and were able to swim freely and actively.

The 28 eggs had on them embryos which were just beginning to show dark stippling on the dorsal parts, and were plainly from two to three weeks younger than the larvæ above described. This is a remarkable case. The eggs were of a late laying. With this case

another must be correlated. On June 8, 1910, I took a female having ovarian eggs 7.5 to 8 mm. in diameter. These might have possibly come to maturity and would then have been extruded to give late embryos like those described above. This certainly would have been the case with the female having ovarian eggs of 20 mm. on June 6, 1907. These cases are, however, isolated ones among scores and even hundreds of normal ones, and are probably instances of extreme variation. On page 36 it is noted that the 28 eggs above referred to were markedly smaller than the normal ones.

## DISTINCTION BETWEEN SEXES.

Except at the breeding season there is no way of distinguishing between the sexes by their external appearance, and so dissection must be resorted to. As the breeding season approaches the fishes begin to show secondary sexual characters. The females develop great swollen abdomens by reason of their tremendously enlarged ovaries filled with 20-millimeter eggs. However, even then there is a chance for error, since a male after a hearty meal of crabs might also present much the same appearance, though he would hardly have such an enormous abdomen as was found in the female from which were spawned 68 eggs averaging 20 mm. in diameter. As the time for oviposition approaches, the anal region of the female becomes highly vascularized, and the genital pore becomes very red and quite protuberant and is noticeably enlarged. This is a sure sign that the eggs are about ripe and ready for expulsion.

More marked, however, is the appearance of the male. Even before the eggs are received, and probably as a sexual reflex, the hyoid region of the male undergoes a marked downward deflection and outpushing (fig. 2, plate 1), and the gill-covers become somewhat distended outward (fig. 3, plate 1). These phenomena develop in all oral-gestating fishes. These outpushings very considerably increase the capacity of an already very large buccal cavity and are an invariable sign that such a fish is carrying eggs, is ready to receive eggs, has just cast out the eggs, or has given up the young.

## METHOD OF TRANSFER OF THE EGGS.

On this interesting point nothing definite is known. In 1858 Green, and in the following year Wyman (1859), reported the finding of eggs of two species in the mouth of an oral incubating catfish of Guiana. From this they concluded that the eggs were disgorged in order to feed and later were taken up again. From this it is not a far cry to Goode's quotation from letters from Silas Stearns (Gill's revision of Goode's American Fishes, 1903): "It (*Galeichthys milberti*) breeds in summer, in June, July, and August. The spawn is deposited in a depres-

sion of the sand and impregnated with milt. One of the parent fish then takes the eggs in his mouth. . . . The eggs are carried in this position until the embryo fish are hatched." Whether this is an observation or a conjecture of Stearns's can not be said. However, the statement is very direct and positive. Smith (1907) quotes it as a fact, and it should be noted here that Stearns seems to have been a careful and accurate observer, and that he had Goode's full confidence.

However, Steindachner (1875), in describing *Arius planiceps*, a catfish from Panama, found that at the breeding season the innermost edges of the ventral fins of the female are developed so as to form a kind of pocket. He conjectured that the eggs are extruded into this, fertilized by the male, and then taken into his mouth. He found a similar structure on the female of *A. kessleri*, the male of which is also a mouth brooder. Moreover, two years before this, Day (1873), writing of the Indian genera *Arius* and *Osteogeniosus*, had described precisely similar structures and had made an identical surmise.

The present writer has sought diligently to ascertain the method of transfer in the gaff-topsail catfish, but in vain. The fish are so large that it has not been found practicable to isolate them in pairs, and the water is too muddy at their breeding-grounds in Newport River for any observations to be made in the open. No structures like those described by Steindachner have been noticed on any female examined. The manner of transfer of the eggs in this fish is still a mystery.

## SEX OF THE EGG-CARRIER.

As has been stated in the preceding pages, and made clear in the article previously referred to (Gudger, 1916), it is always and only the male that carries the eggs. This has been definitely determined for the gaff-topsail by scores of dissections. In this matter *Felichthys felis* falls in line with all other siluroid buccal incubators on record save one. This one exception—probably more apparent than real—is *Arius commersonii*, a sea catfish found in the brackish waters of southern Brazil.

Hensel (1870) first made known this interesting habit in this fish and noted that the male is the incubator. Fifteen years later, von Ihering (1885) confirmed Hensel and concluded his note, which is incidental to a geographical article on the Lagoa dos Patos (in which the fish are caught), by saying that it is the female which carries the eggs. In 1888, von Ihering, in a fuller note on the fish, records the finding of eggs in the mouths of both parents, but thinks this exceptional in the case of the female, while the rule for the male. However, in 1896, he again notes that both parents incubate the eggs.

In the section of this paper on feeding, it will be shown that the female gaff-topsail is cannibalistic in tendency, being occasionally

found with a stomach full of her own eggs or those of her sisters. This fact is believed to offer a solution of von Ihering's dual observations. If this be accepted as true then all known siluroid oral gestators are males.

## SIZE OF MOUTH CAVITY.

While this, of course, varies with the size of the fish, it is always large, since the head of this fish is much larger in proportion to the size of the body than is generally the case in teleosts. This may be easily seen by turning to plate I, figure 1; to the dorsal view of the head, plate I, figure 3; and to the figure showing the mouth with embryos, plate III, figure 7.

Incubating males vary greatly in extremes of size. The smallest ever taken by the writer was 13 inches long over all and carried 4 eggs; while the largest was 23 inches in extreme length but carried no eggs. However, the condition of his hyoid region indicated that he had just given up or was about to receive eggs. The largest number of eggs taken from one male was 55, the fish being 22 inches long. However, the average size of adult egg-carriers is remarkably uniform, running from 18 to 21 inches. On the other hand adult breeding females run larger, from about 19 to 24 inches.

Casts were made of the buccal cavities of 5 nursing males, and 4 of these will now be described seriatim. The first, a cast of plaster of paris, with a volume of 140 c.c., was made from an 18-inch male. The second, also of plaster, is of the mouth of a male 18.75 inches long carrying 11 eggs. Its volume is 135 c.c. The third, of the same material as the preceding, was at the time thought to be the maximum of size since it had a displacement of 267 c.c. Unfortunately the notes giving the size of the fish and the number of eggs carried have been lost. However, these may easily be omitted since full data can be given for the fourth fish, the one from whose mouth 55 eggs were taken.

This fish (22 inches long) was brought to the laboratory that a plaster cast of its enormous "Keimhöle" might be made, but there was not enough plaster in the laboratory to fill it, and there was none in Beaufort. In this predicament the director of the laboratory, Mr. Henry D. Aller, came to the rescue with the suggestion that a cast be made of Portland cement, a barrel of which was at hand. This was done and the fish was held with a towel wrapped around its gills to prevent the escape of the semi-liquid cement until it had hardened. The head was then cut off and put in a dense cedar thicket under a box where it remained until the ants had eaten off all the flesh. Then the cast was carefully freed of the disarticulated bones, shellacked and preserved.

This cast, shown in dorsal, lateral, and ventral views in figures 4, 5, and 6, plate II, is enormous, exceeding in volume both the next largest taken together. Immersed in water up to the deep insinking

made by the sphincter muscles of the œsophagus, its displacement is 580 c.c. The volume of the average-sized egg is 3.75 c.c. Fifty-five eggs would have a total volume of 206.3 c.c. Allowing one-third of this additional for the interstices between the eggs, the total space occupied by the eggs was 275 c.c., leaving 315 c.c. not occupied.

The mouth-cavities of the fish carrying these eggs were very large to begin with, since, as has been noted, the head makes up a large part of this catfish, and these cavities were still further enlarged to accommodate the considerable numbers of immense eggs carried therein. Careful dissections have brought to light the following points: (1) the gill-covers, while outwardly showing no very marked distention, inwardly stand out and away from the gills by about half the diameter of an egg; (2) the gill-arches are pushed outward, giving them a sharp boomerang-like bend in the center; (3) the hyoid cartilages are greatly depressed, forming an outpushing which has been elsewhere referred to as a "double-chin" as shown in the drawing of this fish, figure 2, plate 1; (4), that part of the buccal cavity, behind the pharyngeals and back of the last gill-arch, extending to the point where the sphincter muscle shuts off the œsophagus, is of considerable volume, and in it are always to be found the last eggs, which are always more or less hard to extract. This was particularly noted in the season of 1909. The males could be held up by the tail and shaken without setting all of the eggs free. In a large fish there is space enough back of the last gill-arch for a number of eggs to be held snugly by the mucous lining of the pharynx.

The above measurements, while accurate enough for the casts, can only approximately give us the sizes of the buccal cavities of these fish. That some error is to be discounted is clear from the process of making the casts as given on page 34. The plaster casts are probably too small, owing to too great constriction in the opercular region; while the cement cast is probably somewhat too large, owing to the distention caused by the large amount of heavy cement.

## SIZE OF EGGS AND THE NUMBER INCUBATED.

The eggs, while enormously large, show considerable variation in size, running from 15 to 25 mm. in diameter. Heretofore, however, sufficient measurements have not been made to enable one to say with any definiteness what is the size of the average egg of *any* oral gestator. For the gaff-topsail hundreds of measurements have been made and from them the following diameters are given as covering both normal and abnormal sizes of eggs. It has been constantly observed that the non-fertile eggs of this fish are much larger than the fertile ones. In 1908, at one catch 11 such eggs were taken and measured in 3 diameters. They ran in millimeters, 17 by 18 by 20, 18 by 19 by 20, 18 by 19 by 21, 18 by 20 by 21, 19 by 20 by 21, 21 by 21 by 22, 22 by 22 by 22, 22 by 22 by 23 (two), 22 by 22 by 25, 23 by

24 by 27. The largest fertile eggs measured 18 by 18 by 19, 19 by 19 by 20, 19 by 19 by 22, 20 by 20 by 21. Incidentally these measurements show that the eggs are rarely round, some are markedly elliptical—one 22 by 22 by 26 mm.

To ascertain the average size, the following data are selected out of the large amount available. Of live eggs 138 were measured as follows: Longest diameter only: 17.5 mm., two eggs; 18, nine; 18.5, eleven; 19, thirty-nine; 19.5, ten; 20, thirty-eight; 20.5, eight; 21, nineteen; 21.5, twenty-two. Average of 138 live eggs 18.8 mm. Of preserved eggs, 189 were measured as above: 16.5 mm., three eggs; 17, one; 17.5, one; 18, four; 18.5, two; 19, thirty-four; 19.5, eleven; 20, sixty-four; 20.5, ten; 21, forty-nine; 21.5, five; 22, five. Average of 189 dead eggs, 20 mm. The average of the 327 eggs is 19.5 mm. From the above it will be seen that the largest number of eggs measure 19, 20, and 21 mm. in longest diameter, the 20-mm. eggs being the most abundant—102 out of 327. Normal eggs of this size are shown in figure 8, plate III, while the egg of figure 9, plate IV, is about the same size but has an older embryo.

In connection with the foregoing data, the following measurements should be given, since they are of the smallest eggs, taken as a lot, which have been found in the six years' search. They measured in longest diameter: 15 mm., one; 16, three; 16.5, one; 17, four; 17.5, one; 18, ten; 18.5, one; 19, seven. The average for the 28 eggs is 17.7 mm. This average, however, would be much lower if the last three lots of eggs of normal size were omitted, or even the one last lot only. These eggs were taken on July 21, 1910, and contained embryos having black stippling on the dorsal surface. At the same time there were obtained, from another fish, 5 larvæ which seemed to be from 2 to 3 weeks older than these embryos. All these things lead to the conjecture that possibly these smaller eggs are a lot coming to maturity later and are of a second laying. On these points see page 31.

Not only is there great variation in the size of the eggs, but also in the number carried. Twice I have taken fish with only 2 eggs in the mouth. The smallest incubators caught during this research were 13 and 15.5 inches over all. Each carried 4 eggs. Other small numbers of eggs incubated were 2, 5, 8, 11 (in 2 fish), 13, 14, 15 (in 2 fish), 16, etc. The largest number found was 55 in a 22-inch male. Notable also are 50 (22-inch fish), 45 (taken twice), 38 (22- and 20-inch fish), 36 (from a notably small fish 17.25 inches long), 35 (22-inch), 32 (fish, 20.25 inches long), and numerous catches in the twenties. Once a large male was found with only one egg in his mouth (the only instance anong hundreds captured), but from the great size of the buccal cavity it is probable that other eggs had been thrown out.

That these large numbers of colossal eggs do not, however, entirely fill the capacious buccal cavities of these fish may be readily perceived by referring to the calculations given on pages 34 and 35.

Before leaving this subject brief reference may be made to the large size and to the number of eggs which are carried by other siluroids practicing oral gestation. Evermann and Goldsborough (1902) noted that 39 eggs were taken from the mouth of a 13.5-inch male *Conorhynchus nelsoni*. The average size of the eggs measured was ten-sixteenths by eleven-sixteenths of an inch. Von Ihering (1888) found eggs of 18 mm. diameter to the number of 3 or 4 dozen in the mouths of "large" males of *Arius commersonii* (*Netuma* or *Tachysurus barbus*), a salt-water catfish of southern Brazil. Day (1873) obtained 15 to 20 eggs, 0.5 to 0.6 inch in diameter from the mouths of *Osteogeniosus militaris* and various species of the genus *Arius* in India. Boake (1866) reported the eggs of his Cingalese *Arius* to be about the size of small grapes. Günther (1864) says that the eggs of *Arius fissus* of Cayenne are rather larger than peas. Last of all, but not least, are the eggs of that catfish of Guiana whose native name is *jarra-bakka*, which are declared by Wyman to measure 0.75 inch in diameter. However, it may be remarked that, although much work has been done in recent years on oral gestation in the catfishes of Guiana, none with eggs so large has ever been taken.

## SIZE OF YOUNG AND NUMBER CARRIED.

It is to be regretted that no such full data can be given for larvæ as for eggs carried by the gaff-topsail paterfamilias. Unfortunately but few lots of larvæ were taken, and these larvæ were rarely killed at the time of capture, but were kept that their behavior might be studied, their organogeny worked out, and drawings of them made.

On July 18, 1907, an 18-inch male was caught and from his mouth were taken 21 larvæ. One of these, of average size, after being in 10 per cent formalin for 24 hours, measured: extreme length (point of snout to tip of upper lobe of caudal) 57 mm.; outside width over eyes 11.25 mm.; length of dorsal spine 14.75 mm.; yolk-slit, longitudinal measurement 18 mm., transverse 16.5 mm.

On July 7, 1908, an ovigerous male was taken in whose mouth were found 6 larvæ measuring 53 to 55 mm. long over all. On July 21, 1910, 5 larvæ were taken from the mouth of a male, but unfortunately neither father nor young was measured. Young of about this stage are shown in figure 11, plate IV.

As to the size the young attain before leaving the shelter of the paternal mouth, fairly definite data can be given. In general it may be stated that departure does not occur until the fishlet is grown, *i. e.*, until the yolk-sac has been inclosed by the body-walls. This *a priori* conclusion was verified when, on July 20, 1908, my fishermen brought in a young catfish which they had taken from the mouth of an adult some hours before. In this fish, which was about 4 inches long, the body-walls had completely closed over the yolk of which

there was no outward sign save for a fine aldermanic curve in the abdominal region. The escape overboard of the little fish in the transfer to my bucket forestalled the taking of any measurements. The fishermen (men in whom I have large confidence) told me that towards the close of a haul they had noticed one big catfish and a number of little ones swimming around in the net. The little ones got away but the big one was hastily secured and in his mouth was found the 4-inch young one referred to. A little catfish in this stage of development is portrayed in figure 12, plate IV.

In this connection the following incident may be related, the narrator being long and favorably known to me. Mr. T. E. Adair says that in the early nineties, he and his brother Charles were seining one day off the mouth of Wading Creek in Newport River, when their seine brought in a number of gaff-topsails. These spat out a lot of young some 2.5 or 3 inches long "with a great big yolk dividing the little fish in two." Then he and his brother both distinctly saw the old one open his mouth and the little ones swim into it. He then "took up the big one and poured out a double handful of young ones."

In the section on size of mouth cavity, it was stated that 5 casts had been made but only 4 were described; the fifth cast was that of the mouth of the 18-inch male brooding 21 larvæ as previously noted (p. 37). The volumetric displacement of one of these larvæ, for which measurements have been made, was 4 c.c. That of a slightly smaller one was 3 c.c. scant. Thus the total volume of the 21, if they averaged 4 c.c., would be 84 c.c., or if 5 c.c., only 105 c.c., while the capacity of the mouth as shown by the plaster cast was 120 c.c.

In intimate relation with the number of eggs and young carried by an adult male is the question of how many eggs an adult female may extrude. The largest number of eggs gotten is 55 from the mouth of a 22-inch male. Only one adult female has ever been spawned. This fish is merely noted in my records as being very large (probably about the size of the male above) and from her were obtained 68 eggs. Whatever the facts for smaller fish, it would seem that the largest male does not carry in his great buccal cavity as many eggs as the largest adult female can produce. From which it seems probable that the fish are polyandrous as well as polygamous.

The data at hand indicate that not all the ova extruded are fertilized, and it is quite probable that all the eggs fertilized are not hatched, and that all the young hatched are not matured. However, it would seem from my experiments that, when once the eggs are fertilized, the mortality in the paternal mouth is far less than in the best-regulated hatching-jars. Considerable data on this point have been previously given (Gudger, 1916).

## FOOD AND FEEDING.

From the peculiar dental armature of the gaff-topsail (the teeth being confined to villiform bands on the vomer and palatines and to supra-pharyngeal and infra-pharyngeal pads, and hence adapted for crushing rather than biting, tearing, or holding), one would conjecture that it is not a feeder on fishes, a predatory fish in the common acceptance of the term, but rather a bottom feeder. This finds confirmation in the fact that it prefers a muddy or sandy bottom in muddy water where it finds its food by the help of its tactile organs, the barbels. Moreover, dissections of scores of both males and females make it clear that the gaff-topsail feeds almost exclusively on crustacea. Autopsy reveals an occasional fish (menhaden or croaker), but its principal food is crab, blue crab, eked out with an occasional shrimp. From the much-distended stomachs of sundry specimens, crabs 4 to 5 inches wide have been excised, so large that one wonders how they could have been swallowed. Ocular examination of the contents of the intestines has shown large fragments of the chitinous coverings of crustacea with here and there a claw. On the whole, these contents present a felt-like appearance which persists under an ordinary eye-glass. The microscope, however, resolves this material into minute fragments of chitinous shell, grains of sand, bits of dirt so small that they give the Brownian movement, and immense numbers of crustacean hair-like setæ. There can be no doubt that crustacea large and small form the major portion—perhaps as much as nine-tenths—of the food of the gaff-topsail catfish.

The foregoing observations have been made on females and non-breeding males. Such have always been found in fine full-fed condition, the intestinal tract being plump, well-nourished, fat, distended. Breeding females do not have the distended stomachs of the non-breeding ones, the size of their colossal ovaries forbidding this, but all have been found in good condition.

Breeding males, whether carrying eggs or not, may always be recognized at a glance by their depressed hyoid regions, their "double-chins." For those without eggs it may be conjectured that they have through fright or some mishap given up their eggs, or that they have not yet received them but are prepared therefor—in similar fashion as the uterus of the stingray (*Dasyatis say*) becomes villous to receive the egg even before the latter descends into the oviduct. Such breeding males always have empty, pendulous stomachs and stringy intestines without trace of food in them. This has been found the case in more than a hundred autopsies. From these facts the conclusion is drawn that the ovigerous males of *Felichthys felis* do not feed at all during the time of gestation. Certain it is that no body of any size can pass down the œsophagus without the eggs following.

Holder (1904), however, speaks of the fish with eggs in their mouths biting ravenously at hooks baited with shrimp. But Evermann and Goldsborough (1902) expressed the opinion that *Conorhynchus nelsoni* does not feed during gestation. Day (1873) found no trace of food in the intestinal tracts of either *Arius* or *Osteogeniosus*, both oral gestators of India. Boake (1866) concludes that the Ceylonese *Arius* may feed on microscopic "nutritious particles" floating in the water, but Turner (1867), after studying Boake's specimens, thinks that the amount of food obtained in this way would be practically nil. On the other hand, Wyman, though inclined to think that gestating males fasted, from finding in the mouth eggs of another species was led to believe that the fish might have disgorged the eggs in order to feed, and that on taking them up again the eggs of "another species" were also included. The wording of his sentence indicates that the other species was also a catfish. If this be true it may be conjectured that these eggs were the smaller unripe eggs of the female from whose ovary came the other ripe eggs, extruded and taken into the mouth of the male at the same time with the ripe eggs.

Save Holder (1904), previously referred to, the only other investigator, in all the literature of oral gestation known to me, who has found an incubating male to feed, is von Ihering. He (1888) speaks of catching females of *Arius commersonii* on the hook, but says that males whose mouths are filled with eggs do not take the bait except on rare occasions. Excepting these authors, all writers agree that fishes practicing buccal incubation fast during this period. Such is my conclusion arrived at after 6 years' study and research on the gaff-topsail. In this fish the incubatory period has not been definitely worked out since it has been found impossible to carry early eggs through hatching to the stage of independent life. However, so far as it has been made out by piecing together my observations, incubation continues about 70 days.

Many authors have noted that the incubating fish at or toward the close of gestation are thin, emaciated, worn out with their labors. Unfortunately I have taken but few gaff-topsails in late incubation, and none towards its close, and have noted no striking emaciation in the fishes captured. A few, however, have been rather thin and in poor condition, and moreover it has always been noticed that incubating males taken in June and July do not seem to have much stamina. After being relieved of their eggs they die very quickly, whereas females and non-breeding males are very active and robust, and as a fisherman once remarked "require a good deal of killing" with a fish club before they become quiet. From this it would seem that the duty of incubation bears rather heavily on the male.

The foregoing observations and conclusions have been based on normal fish in normal condition, but before leaving this subject it is necessary to relate and account for certain abnormal cases coming under my observation. These are not only interesting *per se,* but offer a probable explanation for an error of nearly 100 years' standing.

On July 25, 1907, I found in the stomach of an ovigerous male a perfect egg and a fragment of another. Neither showed the faintest trace of the action of the gastric juice. On July 15, 1908, a male was taken and, after removal of the eggs from the mouth, autopsy showed the presence in the stomach of a perfect egg plus several fragments, none of which showed any trace of digestion. In 1909, dissection revealed in the stomach of a male fish a whole perfect egg having an embryo in the same stage of development as those taken from the mouth. This egg was so sound and normal that I expected to see the little fish wriggle on its yolk. Other than this the stomach contained nothing but a whitish ropy mucus. The small intestine was very much reduced in size, inconspicuous in appearance, and was empty but for some yellowish-green watery material. The belly was lanky, but there was no other evidence of wasting or emaciation. In 1910 another male was taken having 2 crushed eggs in his mouth and the fragments of 3 or 4 more in his stomach. Here again there was not the slightest evidence of digestion.

To the writer three possible explanations of the above phenomena offer themselves. (1) In the excitement engendered in the endeavor to escape as the bunt of the seine comes in filled with floundering fish, the male gaff-topsail may give off part of his eggs and swallow others. (2) When the fisherman grasps the fish by the mouth to prevent the loss of eggs, the fish may swallow some in its writhings. (3) Most of the fish just described had been struck on the head with a fish club to quiet them. If there were any eggs between the pharyngeals at this time they would be crushed; further, the blow by reflex action might cause the sphincter muscles of the œsophagus to relax, whereupon both eggs and fragments might be swallowed.

In none of these cases is there any evidence of the eggs having been swallowed as food. Herein my observations and conclusions agree with the only others on record in this matter. Wyman (1859) writes:

> "Besides some nearly mature fœtuses [of *jarra-bakka*] contained in the mouth, two or three were squeezed apparently from the stomach, but not bearing any marks of violence or of the action of the gastric fluid. It is probable that these found their way into that cavity after death, in consequence of the relaxation of the sphincter which separates the cavities of the mouth and stomach."

There are now to be described, and if possible explained, three extraordinary cases which do not come within the above category.

On May 29, 1911, a large fish with a great belly was captured. Touch showed the presence of eggs in this, but they seemed too far forward to be in the ovary. Autopsy made the matter clear. The fish was a male whose stomach contained a great mass of eggs stuck together like a bunch of grapes. These eggs, measuring 18 mm. in diameter, were perfectly fresh and with them was a large number of small eggs and empty follicles, such as are extruded when a female is spawned by pressure applied to the abdomen. Evidently they had been taken up by the male immediately after extrusion by the female and had been swallowed presumably as food. The eggs at this stage are apt to be adhesive and to clump in masses. This was found to be true in the case of the great female spawned artificially, as has been noted elsewhere.

The other two cases may be considered together. A giant fish with an enormous belly was taken on May 25, 1910. Eggs could be plainly felt, but could not be spawned. Dissection revealed that the fish was a female and from her stomach were taken 23 whole and 6 half eggs together with small eggs and partly digested fragments equal in bulk to all the others. On the following day another large fish was taken which also could not be spawned. On performing an autopsy her stomach was also found crowded with 23 full-grown and a large number of small eggs, none of which, however, showed traces of digestion. In both cases it seems probable that the eggs had been swallowed immediately after extrusion and as food; hence we may conclude that the females, unlike the brooding males, are cannibalistic.

These fortunate catches seem to the writer to offer the explanation of the allegation by Hillhouse (1825) and others, especially Bleeker (1858), that certain catfishes are viviparous, the evidence being that they have seen eggs and fœtuses cut out of the bellies of catfishes of various species and genera. These are probably cases in which the eggs and fœtuses had been swallowed by the fish as food.

Possibly the most unique find of contents of stomach was made June 16, 1908. A male taken on this day was found by touch to have some hard object in the stomach. Autopsy revealed a big wooden splinter or fragment some 5.25 inches long. The stomach was empty except for this and a considerable amount of mucus. No suggestion can be offered concerning the presence of this anomalous body in the stomach of this fish.

## FEEDING AND GROWTH OF YOUNG WHILE IN PATERNAL MOUTH.

At the time of hatching, *i. e.*, bursting of the shell, the young measure about 45 mm. over all, but when they leave the mouth and begin an independent existence they are about 85 to 100 mm. long. An early egg, 20 mm. in diameter, after having been in 4 per cent formalin

for 2 years and 6 months, weighed 3.5 grams. A larva with body-walls which had just completely closed over the yolk, the seam of closure only being visible, after being in 4 per cent formalin for 4 years and 3 months, measured 93 mm. and weighed 9 grams. This fishlet was in all respects normal and was just in the stage when the young begin to lead a free life. To make this point clear, the reader is asked to contrast the young fish in figures 11 and 12 of plate IV with the eggs with comparatively early embryos shown in figures 8, plate III, and 9, plate IV.

This increase in length of over 45 mm. (a doubling) and in weight of 5.5 grams (almost a trebling) can not be accounted for by yolk alone—*the young feed in the mouth of the parent.* At some future time it will be shown that the larvæ reared in running sea-water grew faster and when fed by hand were less voracious than those kept in a diluted sea-water filtered many times, the latter feeding ravenously when given bits of oyster. The conclusion drawn in 1907, which has remained unchanged, is that the young feed while in the mouth of the father by filtering out of the respired sea-water, by means of their closely set gill-rakers, minute crustacea to satisfy their hunger. In this way only can their great increase in size and weight be accounted for.

Von Ihering (1888) is the only investigator who has given any data whatever on the growth of the young while in process of brooding. Of *Arius commersonii* he records that the eggs in early development stages average 2.5 grams, while at a time when the larvæ are 60 mm. long they weigh 4.3 grams. The increase in weight, he argues, is due to the intake of nourishment by the embryo.

## LENGTH OF THE PERIOD OF GESTATION.

It is impossible to state this either from observation or direct experiment. It being impracticable, at the time this research was carried on at the Beaufort Laboratory, to isolate the fish in pairs, direct observation of the period of incubation was not feasible. All efforts to effect artificial fertilization proved abortive, nor was I ever able to get eggs in early segmentation stages. Thus it is impossible to fix the time of fertilization, which would give the time of the beginning of incubation. Further, it has been impossible to carry any one set of early eggs through to time of hatching (*i. e.*, bursting the egg-shell) and of the complete closing of the body-walls over the diminished yolk-sac as shown in figure 12, plate IV, at or about which time the young are set free from the paternal mouth.

Confronted by these impossibilities, the best that can be done is to make the closest approximation possible from the data at hand. Now it has been shown in the section on the breeding season that the eggs are "laid" under ordinary conditions of weather (*i. e.*, temper-

ature) between May 18 and 30, and more narrowly between May 20 and 25. There are exceptions, but on the whole the breeding season is seemingly concentrated within narrow limits and the period of incubation has its approximate beginning within these 10 days.

The information at hand is even less definite as to the time of cessation of the care of the male parent. The mortality of eggs hatched in aquaria is very great, and with young eggs all may be expected to die. In MacDonald hatching-jars, which have a bowl-shaped base with water admitted at the center of the base, the eggs are lifted by the incoming current, and all sediment, mold spores, and bacteria are carried off by the overflow at the top. It was thought, moreover, that the use of these jars would conserve the life of the eggs in another way. When the yolk-circulation has extended its plexus of blood vessels over the ventral side of the eggs, if these are allowed to stand in one position, shortly a congestion of these ventral blood vessels is noticed and this is quickly followed by the death of the eggs. In the mouth of the father the constant current of water due to the respiratory actions keeps the eggs free from sediment, bacteria, etc., and presumably keeps them in motion, thus preventing the congestion referred to. It was hoped that in the MacDonald jars the uplifting action of the water would keep the eggs "dancing" and prevent this trouble. To some extent this hope was realized. But even in the best-handled jars, although there was little congestion, the eggs turned white and died by dozens and scores, and in no case was it ever found possible to carry any but late eggs on to hatching. Eggs brought in with young nearly ready to burst the shell could with great care be carried through this dangerous period, and if carried 3 or 4 days further, little trouble was had in bringing them on to maturity. It is interesting to note, however, that there was never any evidence of death due to bacteria, as has been found in the eggs of the toadfish, *Batrachus tau*. For the details of the difficulties met with in the effort to hatch eggs, the reader is referred to the author's 1916 paper.

However, although no definite time can be set for the liberation of the young from the mouth of the father, this can at least be approximated as the time when the body-walls have closed up, as shown in figure 12, plate IV, and the young fish set out to find their own living. In 1907, on July 29, a little catfish was killed and hardened in formalin for 15 hours, at the end of which it measured 81 mm. long over all, while the yolk-slit measured 16.5 mm. long by 2 mm. wide. On August 1, when I left Beaufort, the other fish of this lot in a large aquarium were relatively as active as the adults in Newport River: their babyhood was over.

In 1908 two sets of larvæ were under observation at the close of July. The older ones had the yolk covered over and the slit reduced

to a mere seam on July 27; the younger ones, however, on the same day had the yolk only half covered. On August 8, the day before my departure, the body-walls of the younger had nearly closed over the yolk, while the older had bellies showing no more protuberance than is to be found in the adult shown in plate I, figure 1. These younger eggs were plainly of a late laying.

In 1909 I left the laboratory on July 3 and hence have no data for hatching this year other than that at this time the little catfishes were just beginning to burst their confining shells. However, the fuller data for 1910 show that on July 21 two lots of eggs were taken from a male; one with young embryos just beginning to show dark stippling, while the other lot had embryos with the body-walls covering about half of the yolk; these were from 2 to 3 weeks older than the former. See further on this point page 31, in section on the time of breeding. On July 30 an older fish measured 3.75 inches over all and had the edges of the body-wall united to make a raphe on the mid-ventral wall. The more advanced of the younger lot were able to skate on their yolk-sacs (see figure 11, plate IV), while others were not able to move these yolks which still anchored them to the floor of the aquarium.

All the evidence at hand indicates that the mortality in the ancestral mouth is far less than in even MacDonald hatching jars, and that the young brooded therein become free-swimming earlier. This is undoubtedly due to the fact that they feed while therein as previously described. Only once have I had a fully fledged young one from the mouth of the father. On July 20, 1908, my fishermen, men whom I know intimately and in whom I have great confidence, brought me a catfish about 4 inches long which they had gotten from the mouth of a male. It showed a mere seam on the flattened belly, the yolk being completely gone. No exact measurements could be made, since during the examination the fish jumped overboard and swam away like a flash.

From the data presented above it would seem that the time for the liberation of the young is from July 20 to 30, and under ordinary circumstances about the last week in July. Recalling that incubation begins May 20 to 30, we can approximate the length of the period of gestation as from 60 to 70 days. However, it is clear that the matter of the maximum or minimum limit will be largely if not wholly determined by the temperature of the water and the amount of small crustacea and other microscopic organisms contained therein and available as food for the larvæ.

## THE PURPOSE OF BUCCAL INCUBATION IN THE GAFF-TOPSAIL.

This may be summed up in one word—protection. Let it be recalled that these eggs are of enormous size (the average diameter of 327 eggs being 19.5 mm.) and that when in middle embryonic stages they are very attractive to the eye because of their blood-red vascular yolk investment. For these reasons, if laid as other fish eggs are, they could hardly be expected to escape the eyes of marauding fishes, but if any were so fortunate they would almost certainly be eaten by crabs, those scavengers from which practically nothing escapes. The result would be the inevitable extinction of the species. Moreover, there is yet another danger to which the ova are exposed. These catfish spawn and spend the hatching season on mud flats. If the eggs were discharged on such bottoms they would (because of their great weight, averaging 3.5 grams) sink into the mud and be smothered. To avoid these various dangers, these fish have to do one of two things to insure their perpetuity, *i. e.*, to practice mouth gestation or to lay their eggs in nests which are guarded by one or both the parents. Some fresh-water catfishes have adopted the latter habit; the gaff-topsail has chosen the former.

The whole matter, barring his ignorance of the habit of buccal incubation, has been admirably put by Gurley (1902).

> "It is almost impossible that a mud bottom should be a successful spawning-ground, as the eggs will almost inevitably be asphyxiated. Wherefore, fishes experiencing an impulse to spawn on such bottom will leave few descendants to inherit their delicately sensitive mucous membrane, while those having an impulse to seek harder bottom will transmit to a larger progeny their more roborant mucous membrane. Further, the exception sustains the rule, the only species spawning on mud bottoms being certain catfishes, the males of which excavate nests, and attend to (probably aerate) the eggs, and care for the fry."

## THE ORIGIN OF THE HABIT OF ORAL GESTATION.

The causes leading to the practice of buccal incubation are plainly set forth in the preceding section; the eggs must be guarded in a nest or carried in the mouth, or else the fish would soon become extinct. The gaff-topsail has chosen the latter means to maintain itself. But how has the habit been developed? The answer to this is largely conjectural, but there is a fair amount of data to be adduced upon which to base our conjecture.

It has long been known that some fishes pick up their eggs or young in their mouths for transport from place to place much as a cat does her kittens or a fox her cubs. The writer believes that in this habit are to be found the beginnings of oral gestation. The fishes referred to are members of the families Gasterosteidæ and Osphromenidæ, together with one or two other isolated forms.

The first account to be given is the classic one of Coste, "Nidification des Épinoches et des Épinochettes," published in 1848. After describing the making of the nest and the laying of the eggs, Coste tells how the male *Gasterosteus pungitius* stands watch and ward over the nest until the eggs are hatched, hastening the process by fanning them free of sediment and by helping in their oxygenation at the same time. When hatched, "He does not allow the young to go outside the boundaries of the nest, and if any one does so, he takes it in his mouth and bears it immediately back to its domicile. If, however, the number of deserters increases, he seizes several at one time without hurting them." With regard to the question of feeding during this self-imposed guardianship, Coste adds:

"This animal, which during all the remainder of the year is remarkable for its voracity, suffers an abstinence almost complete during the time devoted to the construction of its nest, the care of its eggs, and the training of its young."

An almost equally charming account is that of Albany Hancock (1854) for *Gasterosteus aculeatus* and *G. spinachia.* In most interesting fashion he describes how he saw the watchful parent with gaping jaws seize the little wanderer, who disappeared therein, as he thought, forever. But to his delight the old fish returned to the nest and deposited the small straggler therein. Then he saw that it was the purpose of the paterfamilias to allow no rambling from the nest. Sometimes the fry were held in the mouth for an appreciable length of time, but they were never harmed.

A similar state of affairs was noted for *Gasterosteus leiurus* by Robert Warrington in 1855. After describing the building of the nest, he says that as the yolk-sacs of the developing young become smaller and their activity greater, "their attempts carried them to a great distance from the parent fish; his vigilance, however, seemed everywhere, and if they rose by the action of their fins above a certain height from the shingle bottom, or flitted beyond a certain distance from the nest, they were immediately seized in his mouth, brought back and gently puffed or jetted into their place again."

Furthermore, if the fishlets are removed by artificial means the father brings them back in his mouth and shoots them into the nest, according to the observations of William Houghton, recorded in 1865. Ransom, in the same year noted the same habit and says of *G. pungitius:* "He seemed to take no food." "The Tinker was almost starving in the midst of plenty." Nor are later observations of this habit lacking if one may credit Becker's notes on *G. aculeatus* published in 1907.

Almost in the Antipodes, we find certain osphromenid fishes practicing similar habits. Many of these make floating nests of foam and mucus in which the male guards the eggs and young. The first

account is from the pen of the indefatigable French aquarist of the third quarter of the last century, P. Carbonnier. Describing a Chinese macropode (1869, 1869*a*), he writes of the male that, after extrusion and fertilization of the eggs:

"He patiently gathers in his mouth the eggs scattered on all sides and carries them under the roof of foam which becomes then for some ten days the object of his solicitude. Without even taking food, he passes his time in watching over the receptacle of his progeny. If one part of the nest begins to empty itself he fills it with new bubbles; he withdraws the eggs where they seem to him to be in too great numbers and carries them into empty places; with blows of his head he disperses the eggs if too much accumulated. When hatching is over he watches with some care over the young embryons; he chases down those which leave the protecting roof, and holding them in his mouth brings them back. He does not cease this surveillance until the too large number of fugitives announces to him that his part is played and that the young family is able to look after its own protection."

Again, in 1872 Carbonnier described similar habits for a "Macropode of China," which may or may not have been identical with the fish described above. In this case, however, both the male and the female took up the young. "I saw the female place in the mouth of the male the slender little [sick] fry which would have certainly perished without intelligent paternal care." Some years later Carbonnier (1875, 1876) describes how the paternal rainbow fish, *Colisa arc-en-ciel*, collects the scattered eggs and embryos in his mouth and transports them to the nest.

Belonging to the same group of fishes is the fighting fish, *Betta pugnax*, whose breeding habits are interestingly described by Waite (1904). This fish is so named because it is bred and trained for fighting by the Siamese. Waite describes in detail its breeding habits, but we are interested here only in its collecting the scattered eggs in its mouth and transporting them to the nest. Waite also (1905) finds a similar habit practiced by the paradise fish, *Polyacanthus opercularis*, the other Macropodes being probably cultivated varieties of this fish. Here again the female assists the male in collecting the eggs and carrying them to the nest made of foam. In one case the fish retained the eggs in the mouth for the space of one minute, this being a matter worthy of particular note in this connection.

And last of all for the osphromenid fishes, we find an identical habit described in Zernecke's Leitfaden for 1907 in the male of *Macropodus viridi-auratus*, which is a cultivated variety of *Polyacanthus opercularis*.

There must now be noted certain isolated instances of mouth carrying by fishes, the last of which brings us close up to the gafftopsail. In the year 1874 Carbonnier described the breeding habits of a fish exotic in France (having been imported from North America), which he called *Fundula cyprinodonta*. Dr. Theodore Gill, however,

declared it to have been *Umbra pygmæa* (*Science*, Dec. 21, 1906). Carbonnier notes that after the extrusion and fertilization of the eggs "the female sucked them into her mouth and appeared to take great pleasure in rolling them around therein, nevertheless she replaced them" whence she had taken them. "When the eggs are found to to be a little scattered, it is clear that the female is no longer their only shield and protector, for the males also suck them into their mouths and pass them from one to another. At this time, the movements which they execute with their fins denote great satisfaction. As they replace the eggs without alteration and without damage, the female shows no air of inquietude; nevertheless at times she turns her head and makes pretense of driving them away." During hatching the female solicitously guards the eggs and carefully removes with her mouth all bad eggs.

One other instance, and we are ready to come to the catfishes. The miller's thumb, *Cottus gobio*, lays adhesive eggs which are guarded by the male. Of it Thomas Peek says (1869): "On the occasion of one of the small fish emerging from its egg, the parent chased it to the bottom of the tank, and, taking it gently in his mouth, replaced it in the cluster."

Further search through the literature would probably reveal other instances of this habit, but incidents enough have been given to make it clear that mouth transportation, as well as gestation, is not altogether unusual. However, similar habits are now to be described in members of the very family of catfishes themselves.

At the 1902 meeting of the American Association for the Advancement of Science, Dr. H. M. Smith, the present United States Commissioner of Fisheries, presented an interesting paper upon the breeding habits of the common yellow catfish, *Amieurus nebulosus*. The particular point in this paper which is of interest just here may be quoted as follows:

"The most striking act in the care of the eggs was the sucking of the egg masses into the mouth and the blowing of them out with some force. The . . . . mouthing operations were continued with the fry until they swam freely, when the care of the young may be said to have ceased. . . . . The predaceous feeding habits of the old fish gradually overcame the parental instinct; the tendency to suck the fry into their mouths continued, and the inclination to spit them out diminished, so that the number of young dwindled daily."

The above is from the abstract of Smith's paper published in *Science* (Feb. 13, 1903). The complete account is to be found in a paper by Smith and Harron (1903), published in the Bulletin of the United States Fish Commission for 1902. In this they say:

"The most striking act in the care of the eggs was the sucking of the egg masses into the mouth and the blowing of them out, this being repeated several times with each cluster before another lot was treated . . . .

"The very young fry were also taken into the mouths of the parents and blown out; especially those which became separated from the main lot and were found in sand and sediment. The old fish would take a mouthful of fry and foreign particles, retain them for a moment, and expel them with some force. After the young began to swim and became scattered, the parents continued to suck them in, and, as subsequently developed, did not always blow them out . . . .

"The fry which were left with their parents continued healthy, but their number steadily decreased. There being no way for them to escape; . . . it was suspected that the old fish were eating their young . . . . They were kept under close observation during the day, and were seen to be fond of mouthing the fry, more especially the weaker ones . . . . They were frequently seen to follow leisurely a fry, suck it into their mouth, retain it for a while, and then expel it, sometimes only to capture it again. There was no active pursuit of the fry, and the tendency seemed to be to spit them out. In one or two instances, however, it appeared that fry taken into the mouth were not liberated, the feeding instinct becoming paramount to the paternal instinct. After all the fry which had been left with their parents had disappeared, in about 6 weeks after hatching, 18 fry were placed in the aquarium one evening, and only 2 of these survived on the following morning."

It seems hardly necessary to argue the question as to the origin of the habit of oral gestation after the presentation of the facts above given. In the mind of the present writer there is no doubt that having begun by taking up the eggs and young for purposes of transportation, the fish have presently learned to retain them for longer and longer periods of time; we have a record of at least one minute's retention; and as the fish which retain their young even for short spaces of time and transport them to safer localities are more likely to leave descendants, through the action of natural selection, these fish and this habit will be perpetuated. Hence we may conjecture that as time has gone on the habit of retention has become more and more fixed until finally oral gestation has become an established habit.

Nor does the matter of abstinence from food offer any difficulty just here. It is known that many fishes which guard their nests do not feed while on such duty, and this is particularly true of the sticklebacks and gouramies. So this fits in well with the conjectural explanation just offered.

To the present writer all the data available lead to the conclusion just set forth, and to it he gives his full adherence.

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3

2

1

1. Lateral view of a female gaff-topsail, 19.25 inches long, drawn from life.
2. Lateral aspect of the head of an ovigerous male gaff-topsail showing the depressed hyoid region.
3. Dorsal view of head of the same fish showing the gill-covers distended to make room for the 36 eggs found in the mouth.

4

5

6

Dorsal, lateral, and ventral views of cast of mouth of male carrying 55 eggs.

7

8

7. Front view of mouth of male *Felichthys felis* incubating eggs.
8. Live eggs of gaff-topsail showing the little fish with heads sunken in the yolk, tails curled to one side, body walls developing, and the extensive yolk vascular system.

9

10

12

11

9. Young gaff-topsail about ready to burst shell, x 3.5. (Natural size of egg, 18.5 mm).
10. Young with tip-tilted tail shortly after being freed from the egg shell, x 1.75. (Natural size of egg, 20 mm).
11. Young in stage when "skating" over the bottom of the aquarium is the only method of progression. x 1.9. (Natural size, 58 mm).
12. Young in free-swimming stage with body walls completely closed over the yolk, x .88. (Natural size, 98 mm).

# IV.

# SPHYRÆNA BARRACUDA; ITS MORPHOLOGY, HABITS, AND HISTORY.

BY E. W. GUDGER,

Of the State Normal College, Greensboro, North Carolina.

Seven plates, five text-figures.

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# SPHYRÆNA BARRACUDA; ITS MORPHOLOGY, HABITS, AND HISTORY.

By E. W. Gudger.

The family Sphyrænidæ, the barracudas, comprises one genus only, *Sphyræna*. The 20 or more species of this genus are found in the warm waters of the tropical and sub-tropical zones all round the world. They are carnivorous fishes, generally of large size, fierce and voracious in habits, the salt-water congeners of the fresh-water pikes.

## GENERAL DESCRIPTION.

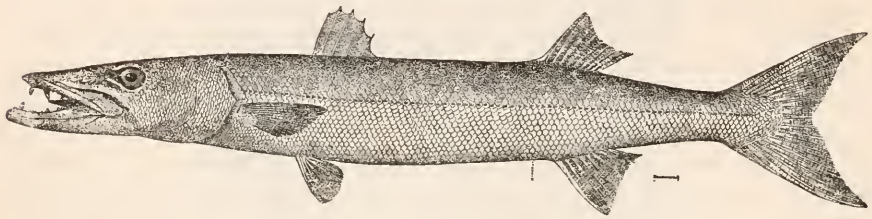
At Tortugas, the great barracuda, *Sphyræna barracuda* (Walbaum), also known in various parts of the West Indies as picuda or becuna, is very abundant in the lagoon. Twelve large specimens have been taken and examined, and scores of others could have been caught if they had been sought. This large fish has a long and powerful body, compressed and rounded, in cross-section having a somewhat elliptical outline. The head is very large, about one-fourth the total length of the fish, is long, narrow, pointed, and flat on top—in short, wedge-shaped. The mouth has an enormous gape, the jaws extending back to a point directly under the eye, and measuring about one-half the length of the head. The lower jaw projects beyond the upper, and both jaws are provided with huge canine teeth. The lower jaw, however, ends bluntly, as is shown in every figure of the fish given in this paper. In marked contradistinction are Fowler's figures (1903) of *S. picudilla* and *S. tome*, in both of which the lower jaw is drawn out into a fine thin point.

All of these points will be made clear by reference to figure 1, plate I, and figures 3 and 4, plate II, photographs of specimens taken at Tortugas and Miami, Florida.* Attention is also called to the spinous dorsal fin, which, with its five rays connected by a thin transparent membrane, is depressible in a groove, thereby becoming invisible. This fin is placed almost immediately over the abdominally located pelvic fins; while the soft dorsal, placed far back, occupies a similar position with reference to the anal fin. Not only are these two fins similar in position and appearance but also in structure, each being provided with a spine in front. The wide separation of the two dorsals and their location over the ventrally placed pectoral and anal fins gives the fish a symmetrical appearance despite its bulky figure. The body ends in a thick, stout caudal peduncle which bears

*The figure on the opposite page (text-figure 1), which is reproduced from Frank T. Bullen's "Denizens of the Deep," represents the barracuda in thoroughly characteristic attitudes. The fishes are well drawn.

the large, rather deeply forked caudal fin, of which the upper lobe is generally slightly the larger. The appearance of this fish gives one the idea of speed and power in about equal proportions. It is of the type of the battle cruiser.

The body of the fish is well panoplied with fairly large cycloid scales. The eyes are large and staring, and are placed about the center of the upper lateral region. The anterior nostril is a small pore at the front end of the supraorbital ridge; the posterior is a slit (0.25 inch long in a 3 feet 10 inch specimen) standing nearly vertical (slightly forward and downward) in front of the eye. Our American authorities (Jordan and Evermann, and Evermann and Marsh) state that the lateral line is straight, but their figure shows that it rises slightly just above the pectoral fin. In my specimens, for the most part, this rise was far



TEXT-FIGURE 2.—*Sphyræna barracuda* (Walbaum), after Jordan and Evermann.

more marked than in their figure, in one fish beginning 2 inches back of the tip of the pectoral. In my largest specimen, however, the rise was only moderately pronounced.

As was noted above, 12 large specimens have been taken and examined, but the fish being so characteristic in structure and markings that it is recognized at a mere glance, fin ray count was made for only one specimen. This fish, an adult, 3 feet 10 inches in length, had dorsal rays v–i, 9; and, i, 8. Jordan and Evermann (1896) give D. v–i, 9; A. i, 9; but their figure has only 8 anal rays. Evermann and Marsh, in their "Fishes of Porto Rico" (1900), make the dorsal rays v–i, 10; and the anal ones i, 8; yet they copy Jordan and Evermann's figure referred to, which has but 9 soft rays in the dorsal. Possibly there is some variation in the number of fin rays. The figure referred to is reproduced herein as text-figure 2.

The table on page 58 gives the comparative measurements of these 12 specimens in inches and the weight in pounds.

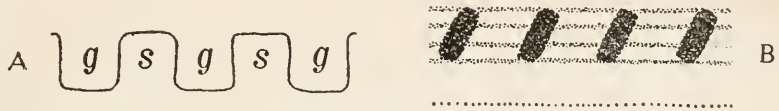
## COLOR AND MARKINGS.

There is considerable variation in the body-color and markings of this big barracuda. In life, specimen No. 11 was on the upper surface a rich dark green, the sides silvery, the belly chalky-white. In the mid-lateral region the green sent down bars into the silvery region,

which in turn sent white bars up into the green, the two forming an interlocking or dove-tailing, as shown in the diagrammatic figure (text-figure 3 A). Unfortunately, the number of these bars was not counted. Specimen No. 10 (3 feet 10 inches long), shortly after being killed, was dorsally black with an iridescent metallic blue in some lights; it had some blue on the sides, lower down was silvery, and the ventral parts were a chalky-white.

Evermann and Marsh (1900) speak of "dark longitudinal streaks along rows of scales above lateral line." This was confirmed on one fish only. Of No. 1, my notes say, "faint dark longitudinal stripes or streaks above lateral line." This was my smallest specimen, 2 feet 1.5 inches in extreme length. The largest Porto Rican specimen was 16 inches long. It seems probable that this is a juvenile marking which disappears with age.[1]

Reference has already been made to the bars found just above the lateral line on each side of fish No. 11. On fish No. 1, lying wholly




TEXT-FIGURE 3.

A.—Dove-tailing of the upper green and the lower silvery colors on the side of barracuda No. 11. (Semi-diagrammatic).
B.—Longitudinal stripes and vertical bars on right side of barracuda No. 1.

above the lateral line and crossing the horizontal streaks at a large acute angle forward, were 18 or 20 dark bars as shown in text-figure 3 B. No. 5 had 18 bars, as noted for No. 1, but no longitudinal streaks were visible. No. 7 had about 18 similar bars, as did No. 8. No. 9 had about 20. No. 10 had 17 on the right side and 18 on the left. No. 11 has already been referred to, and the last and longest specimen either had no such bars or I failed to note them. In the case of No. 6 these notes explicitly state that the bars were lacking. In addition to these bars or oblong more or less rectangular blotches found on the body forward of the dorsal-anal fin region, there were generally present on the lateral hinder parts certain interesting spots to which attention will now be called.

No. 4 had on the hinder half of the right side of the body 15 large black spots, some faint, and some apparently of two run together; but on the left 9 spots only. No. 9, in addition to the 20 black bars above the lateral line on each side, had below the lateral line 23 black spots, some faint and some apparently double. On the left side there were 18. All were mainly behind the anterior margin of the second

[1]Some months after writing the above, Professor W. H. Longley informed me that on July 14, 1916, there was taken out in open water at Tortugas, a little barracuda "about an inch long which was marked with a distinct lateral band of brown pigment running the length of the body through the eye."

dorsal. No. 10 had 18 black spots on the right and 14 on the left side. These were below the lateral line and extended from a point just anterior to the anal back to the caudal peduncle and on this some were found above the lateral line also.

No. 12 had on the right side about 15 spots; some large, some small; some distinct, some faint. On the left side there were 2 large spots about amidships, and behind these about 6 small indistinct spots. Furthermore, interesting to note, there were on the ventral surface of the body, on the median line, between the anal and caudal fins, quite a number of dark spots. These were not noticed on any other fish.

Evermann and Marsh (1900) speak of "usually from one to several small, very dark brown spots, sometimes black, scattered irregularly

| Measurements in inches. | No. 1 | No. 2 | No. 3 | No. 4 | No. 5 | No. 6 | No. 7 | No. 8 | No. 9 | No. 10 | No. 11 | No. 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Length to— | | | | | | | | | | | | |
| tip of caudal | 25.5 | 29 | 30.5 | 34.3 | 35 | 37.5 | 40 | 40.8 | 43 | 46 | 49 | 55 |
| fork of caudal | ..... | ..... | ..... | 32 | ..... | 34.5 | ..... | ..... | 40 | ..... | 46 | 52.8 |
| base of caudal | ..... | ..... | ..... | 29 | 30 | 32 | 34 | 35.5 | 36 | 38 | 39 | 47 |
| anterior base D. II | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 29 | ..... | ..... |
| Length of head | ..... | ..... | 8 | 9 | ..... | 9.5 | ..... | ..... | ..... | 12.5 | 13 | 15 |
| jaw | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 7.5 |
| spine 2 of D. I | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 3.9 |
| Girth back of pectorals | ..... | 9.5 | ..... | ..... | ..... | ..... | ..... | ..... | 14 | 15 | ..... | 20.5 |
| at front edge D. I | 9 | ..... | ..... | 11 | 12 | 12.8 | ..... | 14 | ..... | 14 | 16 | 22.5 |
| at base of caudal | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 7 | ..... | 8 |
| Depth | ..... | 3.8 | 4 | 4 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 8.8 |
| Diameter of eye | ..... | ..... | 1 | 1 | ..... | 1 | ..... | ..... | 1 | $\frac{7}{8} \times \frac{9}{8}$ | 1 | 1.5 |
| pupil | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | $\frac{9}{16}$ | ..... | ..... |
| Spread of pectorals | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 11.5 | ..... | ..... |
| D. II and anal | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 11 | ..... | ..... |
| caudal | ..... | ..... | ..... | ..... | ..... | ..... | 10 | ..... | ..... | 13 | ..... | ..... |
| Weight—pounds | 2.5 | 4 | ..... | 6 | ..... | 9 | 9 | ..... | 13 | 17.5 | 21 | 38 |

on the side." They also say that the young have dark irregularly shaped blotches or bars sometimes disappearing with age. However, from a study of my specimens described above it would seem that this conclusion does not apply to the Tortugas form. Further it is interesting to note that No. 2 (2 feet 4 inches in extreme length) had but 4 spots on the right and 3 on the left side, some of these being very pale. Then again No. 6 (3 feet 1.5 inches outside measurements) had no spots at all. This may have been *S. guachancho,* which is described as being devoid of any color markings whatever, lacking "regular bars and scattered spots." In this connection it is of interest to note that Temminck and Schlegel (1850) in writing of Japanese barracudas say that the young of *S. vulgaris* have the upper parts covered with brownish marblings and that on the lateral line there is often found a range of dark spots, oblong and rather closely crowded.

The following are descriptions of the markings of four small barracudas taken at Tortugas in the season of 1917, which were kindly sent

to me by Dr. A. G. Mayer. In transit the bottle containing them was broken and they reached me in a dried condition, but with their color markings quite clear and well defined. No. 1, measuring 2.6 inches from tip of snout to base of caudal, has, between that point and the hinder edge of the opercle, about 9 dark blotches which extend across the dorsum and down to the belly on each side. Another fish of the same length, but hardly so bulky, has about 7 of these saddle-shaped bands. A third, 2.35 inches to the base of the caudal, has about 6. The last and smallest (2.25 inches) has 7 bands, possibly the most definitely marked off of all. In addition to these bands noted, there is another, not quite so clear, extending from the fore part of one opercle across the back to the other gill-cover. Again, on the dorsum, across the base of the skull, all four specimens show a dark blotch.

These bands are especially large and are somewhat irregular in shape in the region of the lateral line on each side. On the median line of the dorsum, especially in the region of the second dorsal fin, these bands run together, giving these parts a very dark, even black appearance. There can be no doubt that, as the fish grows older, the dorsal connection disappears and the lateral parts of the bands are left as the dark bars or splotches described above and shown in figure 1, plate 1.

These colors referred to above were noted on my fish after death. In life the color of the fish readily accommodates itself to its surroundings. A large barracuda basking near the surface of the water in the neighborhood of a coral head, a buoy or a channel stake, appears much as a ghost fish, a shadowy wraith. Another lying near the bottom over coral sand will so accommodate itself to its environment as to be almost unnoticeable so long as it remains quiet. Wood-Jones (1912) says that it is the hardest of all sea fish to see.

## JAWS AND TEETH.[1]

The mouth parts of the barracuda deserve attention both for themselves and because they do not seem to have been adequately described. The mouth is very large, being in length nearly half of the head and having a large gape. Together with this, the projecting lower jaw, the enormous canine teeth, the large glassy staring eyes, give the fish an aspect of ferocity which is not belied by its habits, as will be shown later. It has been fittingly compared to a bull-dog, and Saville-Kent (1893) notes that at Moreton Bay, Australia, it is called *dingo* because of "its formidable array of teeth."

The lower jaw is longer than the upper, projecting notably as a conical fleshy mass of tissue which, if on the upper jaw, would form a decided snout. Dissection of this jaw in the fresh specimen revealed

[1]The material on which I have based my observations for this section consists of four dried heads from Tortugas (dried with the mouths distended) and one fresh head sent to me packed in salt from Miami, Florida. For this last specimen and for previous similar favors I am indebted to Mr. John Mills, of Miami.

the following interesting structure: The rami of the mandible are as usual united at the apex by a mass of cartilage, but what is unusual is that this cartilage projects forward as a considerable lump which, covered by flesh and skin, gives the lower jaw the appearance shown in figures 3 and 4, plate II, and figures 7 and 8, plate III. For the dissected jaw see figure 13, plate IV. It should be noted, however, that in cutting away the flesh and skin some of the cartilage was unwittingly removed, hence the projecting mass is not as great as in nature. This conical lump forms the terminal part of the rather thin fibrous lip of the lower jaw. This lip is freely movable and has, fastening it to the skin of the jaw, a number of short oblique backwardly trending slips of tissue. These allow free motion of this lip. For these structures see figures 4 and 8, plates II and III.

Turning now to the upper jaw, it is readily seen that the premaxillaries lie outside of and are separated from the maxillaries by a deep groove. In front, the symphysis of these bones is, like that of the lower jaw, covered by a mass of soft tissue. This mass, however, is much smaller than that of the lower jaw, does not form such a conical projection, and is comparatively thin and upturned. At the very point on the median line this is hollowed out into a deep pocket for the reception of the great fang of the lower jaw. To aid in the formation of this cavity, the terminal portions of both premaxillaries are hollowed out to the point of union to form a little bay. Viewed dorsally, the maxillaries seem to lie above and (in the hinder region) outside of the premaxillaries, but in front they swing toward the median region. Viewed from below, the true situation is revealed; posteriorly they lie outside the premaxillaries, but about one-fourth the distance forward they cross over these bones and come to lie inside and are united by tissue in the region of the hinder group of great fangs on the premaxillaries. Attached to each premaxillary is a thin fold of skin forming a less pronounced and less movable lip than is found on the lower jaw. These structures are seen in figures 7, plate III; and 11 and 12, plate IV.

The articulation of the upper jaw to the skull is entirely unique and hence worthy of description. The premaxillaries are non-protractile and are almost incapable of motion. The maxillaries, however, are so hinged onto the anterior end of the cranium as to allow the tip of the upper jaw to be raised in a vertical plane. This interesting articulation is shown in figures 11 and 12, plate IV. The vomer has each shoulder beveled off dorsally and anteriorly, and in front there is a stout spine rounded off on the upper surface and the anterior end. The palatines send forward stout processes rounded in front, flattened below and especially on the inner edges. Between these two processes above and the projecting point of the vomer below there is seen a considerable space, if one looks at the skull laterally. In a ventral view the maxillaries are seen to have just behind their symphysis a pair of

pockets or recesses; a dorsal one as wide as long, and a shallow ventral one lying anterior to the other. The roof of the larger recess is made by the nasals, which are united by and imbedded in a mass of cartilaginous material. The sides of this pocket are formed by two rounded backwardly and slightly inwardly projecting prominences of the maxillaries. Viewed from above, the anterior ends of the maxillaries, just outside the processes described, are hollowed out into shallow cavities whose use will be described below. Figures 11 and 12, plate IV, show these structures both from below and from above.

In articulation these bones fit together as follows: the forward prolongation of the vomer fits into the posterior and dorsally placed cavity between the maxillaries; the backwardly projecting processes of the premaxillaries fit into the spaces between the shoulders of the vomer and the forwardly projecting processes of the palatines; while the united nasals lie dorsal to the frontal process of the vomer and between the forwardly projecting horns of the palatines; and lastly the flattened and rounded ventral surfaces of these same horns fit into the grooves excavated into the anterior dorsal surfaces of the maxillaries. Thus there is formed a beautiful joint allowing little motion laterally but considerable in the vertical plane. However, the union of the right and left halves of both maxillaries and premaxillaries by ligaments and cartilage allows a widening of the upper jaw at the angle of the mouth, as will be shown below.

The rami of the lower jaw are likewise united in front by cartilage and connective tissue, and behind they are hinged onto the quadrates. These in turn are immovably attached by suture joints to the palatines. These latter bones are hinged like a door or the lid to a chest, posteriorly to the prefrontals and anteriorly to lateral projections of the vomer. In widening the mouth, the upper and lower jaws spread apart behind and the quadrates and palatines swing outward and upward. This takes place at the same time that the lower jaw drops downward while the tip of the upper jaw is raised. All this results in giving the barracuda an enormous gape, a necessity for a fish which preys on other large fish and which swallows its food in large fragments. These points are well shown in figures 5, plate II; 7, plate III; 11, 12, and 13, plate IV.

The lower jaw is filled with knife-like canine teeth set palisade fashion just inside the lip-like membrane. These are small in front but larger in the middle and posterior parts. They point slightly backward, especially those in rear. Their numbers for my five specimens appear in the accompanying table, the dried heads being taken in the ascending order of size. The + teeth are the small ones at the

| Specimen. | Left. | Right. |
|---|---|---|
| Fresh..... | 13+7 | 11+4+3e |
| Dried No. I... | 11+5 | 12+2 |
| II.. | 13+4 | 11+3 |
| III. | 14+3 | 16+5 |
| IV. | 17+4 | 12+6 |

front of each ramus of the jaw; those marked +e are in the act of erupting. Two factors seem to account for this variability. First the size of the fish; the larger the fish the greater the number of teeth. The fresh head was unfortunately not measured, but a study of the teeth and comparative measurements of the bones show that it was about the size of the dried head No. III, and possibly a little larger. The second factor relates to the number of teeth that have been broken off without sufficient time having elapsed for their being replaced. This is particularly true of dried head No. IV, where on the right side several teeth have been broken off. Figure 13, plate IV, from a photograph of the lower jaw of the fresh specimen, will make these points clear.

In front, at the symphysis of the rami of the lower jaw, is a huge fang, bowed on the front edge and slightly hooked backward. This was single in each of my five specimens, on the right side in four specimens and on the left in one. Two of these teeth might be expected but one seems to be always broken off. This matter will be discussed later, but it should be noted here that this tooth is always inclined toward the vertical median plane of the head and jaws—that on the left side towards the right and that in the right *vice versa*.

The upper jaw has in front at the apex, under the snout, a group of huge knife-shaped fangs, two, three, or four on each side, not two pairs as Jordan and Evermann state. The two anterior of these generally point about straight downward, while the posterior ones are sharply hooked backwards. All are convexly bowed on the front edge. These teeth may be seen in nearly every figure of the fish and of its head given in this paper. The accompanying table shows their numbers in my five specimens.

| Specimen. | Left. | Right. |
|---|---|---|
| Fresh..... | 3 | 2+3e |
| Dried No. I.... | 2 | 2 |
| II... | 2 | 2 |
| III.. | 2+1e | 2 |
| IV.. | 3+1e | 2+1e |

Implanted on the palatines in palisade fashion are a number of large, pointed, lancet-shaped teeth, in structure and arrangement very similar to the mandibular teeth but much larger. These are largest in front and decrease in size backward, becoming very small at the rear. The most anterior ones are but little if any smaller than the great fangs and on each side the series runs backward in line with these fangs. These teeth have, however, no physical connection with each other, there being a wide hiatus between them, as may be seen in figure 12, plate IV. The accompanying table gives the numbers of these teeth for each specimen. The + teeth are the small ones at the rear, while +e indicates teeth just erupting. Here again, it will be noted that the larger the specimen the larger and more numerous the palatine teeth.

| Specimen. | Left. | Right. |
|---|---|---|
| Fresh..... | 6+2+2e | 4+1+1e |
| Dried No. I.... | 4+2 | 5+3 |
| II... | 7 | 6+1 |
| III.. | 7+2 | 9+2 |
| IV.. | 10 | 8+1 |

Closely set in palisade fashion, beginning about opposite the space between the first and second great fangs, are the small knife-like teeth of the premaxillaries. These teeth, pointing slightly backward and extending clear to the angle of the mouth, give the upper jaw a very saw-like appearance, as may be seen in figure 8, plate III. The data tabulated herewith would seem to show that the number of these teeth is fairly constant, the discrepancies being chiefly due to teeth broken off and not yet replaced.

| Specimen. | Left. | Right. |
|---|---|---|
| Fresh..... | 30 | 44 |
| Dried No. I.... | 45 | 34 |
| II... | 41 | 29 |
| III.. | 41 | 47 |
| IV.. | 38 | 47 |

An interesting point was passed over in the dried heads and seen only when the fresh head was dissected—that the teeth of the lower jaw, those of the premaxillaries, those on the palatines, and even the great fangs under the snout; all the teeth in the mouth, except the solitary fang of the lower jaw, are set "overlapping." That is, in every case, where the teeth are crowded, the front edge of every tooth rests on the outer side of the tooth before it, and its hinder edge is set on the inside of the tooth behind it; going from *behind forward*, the teeth over-lap like the shingles on a roof. This is especially apparent where new teeth are ready to erupt. Reference to figures 12 and 13 on plate IV, photographs of the cleaned-off jaws, will make this plain.

When the mouth is closed, the parts of this formidable dental apparatus are approximated sausage-mill fashion, as follows: The teeth of the lower jaw fit into deep grooves between the premaxillaries and palatines of the upper jaw and the big anterior canine fits into the pocket of the upper jaw which has already been described; the premaxillary teeth of the upper jaw come to rest against the lip-like membrane lying just outside the great teeth of the lower jaw, while the huge palatines fit into a wide, deep space between the lower jaw and the tongue, and finally the big anterior canines are received into special recesses in the membrane lining the anterior part of the floor of the mouth just behind the symphysis of the mandibles. Held in such teeth no fish can escape save by leaving part of itself behind.

The sausage-mill approximation of these teeth will be clearer after an examination of figures 6, plate II; 12, plate IV; 9 and 10, plate III. The particular point to be noted is the presence of the mandibular breathing valve, and in its forward part the depressions in it which accommodate the great canines of the upper jaw. However, the modification of the mouth parts to fit these huge teeth does not end here, but extends to the very bones themselves. In figure 13, plate IV, the reader will discern on the inside of each ramus of the lower jaw just behind the junction an excavation in the bone. These are to receive the points of the great canines of the upper jaw.

There are no teeth on the vomer, but on the tongue is a number of rows of small, sharp-pointed recurved teeth which must materially aid in the swallowing process, as do the large number of small teeth covering the pharyngeals above and below and the inner edges of the gill-arches. These are quite necessary, since the great barracuda chops its prey (if of any size) into large fragments which are swallowed whole. In addition to the structures described, there is a large breathing valve in the upper jaw, just posterior to the four great canines and anterior to the palatine teeth. Below, a similar structure is found just in front of the tongue. The tongue has considerable freedom of motion.

On the under side of the lower jaw, just behind the point of junction of the mandibles, are two round apertures leading into blind sacs extending both backward and forward some little distance. What function these subserve is not known to the writer. They are shown in figure 6, plate II.

Before leaving this subject it may be of interest to give the sizes of some of these great teeth. In fish No. 10 (3 feet 10 inches long), the single tooth at the apex of the lower jaw measures 13 mm., the big upper front teeth are 15 mm. long free of the gum, and the knife-blade teeth implanted on the palatines run from 9 to 13 mm. The large teeth of specimen No. 12 (55 inches long), which is No. IV of the tables of teeth, have for the most part had their points broken off and hence their measurements, generally speaking, do not show up so large as they should. Thus the big lower tooth measures only 11 mm., while the upper ones run from 12 to 14 (tips broken) to 17 and 18 mm. (perfect teeth). The palatine teeth of this fish run from 9 to 16 mm. These measurements, it must be understood, are all made from dried specimens and may possibly be slightly greater than in the freshly caught fish. When the flesh was cleaned off of the fresh head, on the lower jaw the big anterior tooth (tip broken) measured 10 mm. and the great chopping teeth further back ran from 6 to 9 mm., averaging about 7 to 8 mm. The great fangs of the anterior upper jaw measured 11, 13 (two teeth), and 14 mm. (Two other teeth were at the point of erupting.) The four great incisors on the right palatine measured 12, 14, 8 (tip broken), and 10 mm. from before backward. Similar measurements for the four corresponding teeth on the left palatine were 12, 11, 11, and 9 mm.

Figure 5, plate II, shows the number and relative position of these great teeth of the upper jaw. Some idea also can be gotten of the size, shape, and position of those of the lower jaw. The photograph was taken looking into the mouth from behind. The two inner groups of teeth are the great fangs on the premaxillaries. The outer groups are the huge knife-shaped teeth on the palatines.

Inspection of figures 12 and 13, plate IV, shows that the teeth are set in alveoli or sockets in each ramus of the mandible and the premaxillary, and in each palatine. These teeth are polyphydont—that is, they are replaced by new teeth as soon as they are worn down, broken off, or become loosened in their sockets. In some socketed teeth the succession is vertical, *i. e.*, the new tooth is formed in the same socket as the old one and grows out at the same aperture. This is by virtue of the fact that the base of the old tooth is absorbed and the new tooth thus comes to lie below it and to take its place. In other fishes the new tooth succeeds its predecessor, growing side by side with it or its stump.

In the great barracuda the teeth are set in sockets, out of which they grow by multiplication of cells at their pulpy bases. Room for the new teeth is often made by the old teeth being broken off, whereupon the root is resorbed and a new tooth erupts alongside the first to take its place. This state of things can be seen in the photographs of the skull of the specimen from Miami, as shown in figures 12 and 13, plate IV. In the figure of the lower jaw, the fang at the terminus of the left ramus has been broken off and already one sees the chink through which the new tooth will emerge. In figure 12, of the upper jaw, we have a similar state of affairs. The left front fang has been broken off, the one next to it has become loose in its socket and in the space between the two is seen the hole out of which the new tooth will come.

Closer inspection of figures 12 and 13, plate IV, will show some two dozen similar cases among the premaxillary, mandibular, and palatine teeth. All stages can be made out from the recently broken-off stumps to the half-grown replacing tooth. This is the reason for the variable number of great fangs at the apex of the upper jaw. Some of these in the cleaned head, it should be noted, were so loose in their sockets that they had to be glued in to prevent their being lost. A similar state of affairs is revealed by a close examination of the jaws of the three dried heads. The study of the succession of teeth in this fish would be of both interest and value. It would, however, have to be undertaken where there was an abundance of fresh material.

Before taking up the literature of this phase of the subject it is well to emphasize the fact that all my specimens and their figures show but one fang at the symphysis of the lower jaw. For this see the figures of the dried heads on plate III; and figure 13, plate IV, showing the teeth of the fresh specimen from Miami. These single fangs are always inclined toward the median line, the ones situated on the right side are inclined towards the left, and *vice versa*. Inspection of the largest dried head and of the fresh specimen, however, shows that the left tooth has only recently been broken off; while in

dried head No. III, a new fang is just ready to erupt on the right side. Apparently two teeth belong at the apex of the lower jaw, but only one seems to be present at any given time. This point will be taken up again after the literature of the subject has been reviewed.

The earliest writer whom I have found to give any accurate description of the jaws and teeth of *Sphyræna* is Rondelet (1558).* Writing of the European form, the spet, he says:

"The lower jaw is longer than the upper, ends in a point, and receives the upper jaw into itself. . . . It has strong pointed teeth curved inwards like those of the Muræna. On the upper jaw there are four, and on the palate are two rows of teeth. At the center (apex) of the lower jaw there is one tooth greater than all the others, which enters into a cavity in the center of the upper jaw made on purpose to receive it."

Even clearer and more explicit is the Roman physician, Salviani, whose folio work on fishes appeared in the same year as that of the Latin edition of his contemporary. He writes:

"The upper jaw is obtuse and shorter, the lower acute and longer. As a result, the point of the wedge-shaped beak is constituted only of the extreme part of the lower jaw; and into the lower and longer maxilla, the shorter upper jaw fits when the mouth is closed. Each jaw is fortified with teeth, the upper with larger ones, the lower with smaller; and in the middle of the anterior part of this lower jaw, indeed in the very hiatus of the mouth, there stands out one tooth the longest and sharpest of all. This, when the mouth is closed, is so received into a foramen in the anterior and membranous part of the upper jaw, that this projects a little on the outside."†

These descriptions, though made from the Mediterranean species, are more accurate for our fish than is Sloane's, even though his was written from the West Indian form found at Jamaica. Sloane says (1707), of a barracuda 15 inches long and hence immature:

"The under jaw had two Rowes of small Teeth, and one long one at the End in the Middle, the upper had one Row of small teeth on the outside and another within of long ones."

Catesby's description (1754) is also very imperfect. For his fish see figure 16, plate V. He simply says of Bahama specimens:

"The upper jaw is armed with four large teeth, placed at [opposite to] the fore part of the under jaw; next the head are placed ten smaller teeth, being five on each side; and in the fore part of [the lower jaw] . . . grows one single large tooth."

Patrick Browne (1756) found two large canines at the apex of the lower jaw, which he notes was the longer. The mouth is described as very large, the jaws especially so. These are filled with many oblong lanceolate teeth, "whereof the two foremost [on the lower jaw] pierce

*The first edition of Rondelet's work was published in Latin in 1554.
†This is faintly shown in Salviani's excellent figure.

through so many sockets formed in the tips of the upper jaw, while others lodge on either side of the opposite teeth." He seems to be the first to note the presence of teeth on the tongue and of the two lower fangs.

Fermin (1769) contents himself with saying that the jaws are filled with long and trenchant teeth which nothing can withstand.

Parra's interesting book on Cuban fishes, published in 1783, contains a pretty fair description of the dental apparatus of the West Indian barracuda, perhaps the best up to date. His figure, however, is crude. See figure 17, plate v.

His statement reads:

"In the upper jaw these fish have in front four teeth larger than the others, and posteriorly three or four others also large: on the external lip of this jaw they have a row of teeth small in size. In the lower jaw they have one in the middle, also large, which corresponds to a space which has been noted in the upper jaw. . . . there appear on the margin of the lower jaw, teeth small at first but which soon grow larger and articulate with the large and small teeth of the upper jaw. To their sharp edges and position as described is due the fact that these animals cut like a knife when they bite."

The most accurate description of the jaws and teeth of fishes of the genus *Sphyræna* that I have seen is that by Cuvier and Valenciennes, in the third volume of their *Histoire naturelle des poissons* (1829). In speaking of the Mediterranean form, *S. vulgaris*, the common spet, they note that the lower jaw ends in a fleshy point, that the tip of the upper is truncated to adapt itself to the curve of the lower, and that both have membranous lips outside the teeth. Cuvier and Valenciennes's description of the jaws was not read until months after my own specimens had been described, yet the reader of this paper will find the descriptions almost interchangeable. They say:

"The intermaxillaries [premaxillaries?] have along their edge a single row of very small teeth, numerous and sawlike; but at their anterior extremity and a little inside, they each have two large ones, one behind the other, compressed, trenchant, a little arched and pointed. A little further back and at some distance from the intermaxillary teeth, but in the same line, there are on each palatine three or four equally large, cutting and pointed, but not arched teeth; then there follow backward along the length of each palatine twelve to fifteen other teeth, very small and shaped like saw teeth, after the fashion of those on the intermaxillaries.

"On the lower jaw there are two strong cutting teeth, pointed and hooked, which correspond in this anterior region to the four on the upper jaw. The fish often has only one and this gives it the air of never having had but one at the end of the lower jaw. Along each side of this jaw one sees at first sight a series of a score of very small teeth of which the hinder ones become very large and trenchant but not half equalling the great palatine teeth which are directly above them. When the mouth is closed the lateral teeth of the lower jaw enter into the interval between the intermaxillary and palatine teeth of the upper. The vomer has no teeth."

Of the great barracuda, Cuvier and Valenciennes give an excellent colored figure accompanied by a line drawing of the jaws and teeth. The former figure is reproduced as figure 18 of plate v, while figures 19 and 20, plate vi, show both the line drawing referred to and the head of the colored figure. The reader is particularly requested to contrast the figure of the jaws and teeth with the photographs of Florida specimens. Cuvier and Valenciennes note that the great teeth are very large and non-arched, but their figure has them (especially the upper ones) curved backward. Of the other teeth they say:

"Each palatine has a number of large teeth, which may range from five or six to ten or twelve, without any little ones, either in their intervals or farther back. At the most each has three or four small ones, which are only seen in young specimens or when one cleans off a skeleton. Hence the edge of this bone is sharp and smooth."

In their full-length figure the great teeth above and below are hooked backwardly; there is only *one* big canine below but two above. In the line drawing two lower canines are seen straight and unpointed, while the four big upper ones are backwardly hooked.

Louis Agassiz (1843) not only figures the jaws and teeth of *S. barracuda* but the skull and skeleton as well. His beautiful figure, which in the main points is technically correct, is herein reproduced as figure 21, plate vi, while figure 22, plate vi, is an enlarged photographic copy of the skull and adjacent parts. The one point criticizable is that the pelvic fin is possibly placed slightly too far forwards. After noting that all the parts of the head are much elongated Agassiz says:

"The intermaxillaries have a single row of small teeth on their lateral border, but in front and a little inside there are two very large ones, compressed and very trenchant, slightly bowed and very pointed, accompanied sometimes by one or by two teeth much smaller. Farther back and on the same line, the palatines bear a series of five or six equally large, sharp and pointed teeth, not bent but for the most part like lance heads. Succeeding also to these on the length of the palatines are twelve or fifteen teeth much smaller and serrated like those on the intermaxil aries. The lower jaw has only two large trenchant teeth, pointed and bent, at the anterior symphysis of the branches of the mandible, which correspond to those of the upper jaw. Along each arm of the lower jaw, there follows each other a series of teeth, trenchant, straight, pyramidal in appearance, more or less large and more or less elongated. These correspond to the grand palatines and fit in between these and the intermaxillaries when the animal closes its formidable mouth."

To recapitulate, Rondelet (1558) and Salviani (1554) each found a single tooth at the symphysis of the branches of the lower jaw; so did Sloane (1725) and Catesby (1754) and Parra (1787), while Büttikofer (1890) found but one in the lower jaw of *S. jello* caught off the coast of Liberia. Jordan and Evermann (1896) call for and figure but one. Fowler (1903) found but one in *S. tome*. Bullen (1904), in his very

spirited figure (text-figure 1), shows but one fang. Wood-Jones (1912), in his photograph (figure 2, plate I) of a giant specimen from Cocos-Keeling Islands, shows but one tooth. My five specimens, as their photographs show, had but one fang each. On the other hand Browne (1756) speaks of two teeth at the symphysis of the lower jaw as does Guichenot in his "Poissons de Cuba" (1850). In describing the spet of Mediterranean waters, Cuvier and Valenciennes (1829) distinctly say that at the point of the lower jaw are two large, strong, curved teeth. Of the great barracuda they say that the dentition is like that of the spet. Their full-length figure of *S. barracuda* shows but a single tooth at the apex of the lower jaw, but their line drawing of the head found on the same plate shows two straight fine-pointed teeth. The single tooth in the other figure is, however, correctly hooked backward. Agassiz (1843) likewise says that the lower jaw has two great teeth at its apex, but his figure shows only one. (See figure 22, plate VI.) The last to be quoted is Day (1865), who says that there are two large canines in the anterior part of the lower jaw of *S. jello* of India.

It is interesting just here to note that Cuvier and Valenciennes quote Plée as saying that he has seen great numbers of young barracudas not more than 6 inches long and that "all lack the tooth of the lower jaw." The following data, however, may be given for specimens hardly more than one-third as long as Plée's. The four little barracudas taken at Tortugas in 1917, and described on page 59 for their color markings, have the great tooth of the lower jaw present and exposed for study by reason of the shrinking of the tissues at the tip of the upper jaw. The largest and bulkiest fish (2.6 inches long to the base of the caudal) has but one lower anterior tooth, the right. All three of the others (measuring 2.6, 2.35, and 2.25 inches) have but one each and that the left tooth.

After thinking on the matter for some time, it became clear to me that since the lower jaw is bilateral and since there is one fang at the external end of one ramus of the mandible, there is due to be one at the other. When the head of the fresh specimen from Miami was cleaned off, there (in the proper position), was the base of the broken-off left fang. A little dissection of the largest dried head revealed a precisely similar state of affairs. Removal of a lot of tissue at the apex of the lower jaw of dried specimen No. III showed a new tooth nearly ready to break through; and in the smallest dried head the stump of a broken-off tooth was found.

From a consideration of the foregoing facts it is clear that the great barracuda normally has two great teeth at the apex of the lower jaw, but for some unknown reason only one is commonly found, the one or the other being broken off. It would be of no small interest if the reason for this could be ascertained.

## MANNER OF BREATHING.

In the preceding section, reference has several times been made and attention has been called to the figures of the breathing valves. These structures are developed to such a degree in the barracuda, that the fish is enabled to breathe with its mouth open or at most only partially closed. The head, including both the upper and lower jaws, is remarkably elongated and sharply pointed, as may be seen by reference to figures 3 and 4, plate II. Across the narrow anterior end of the roof of the upper jaw is stretched a fold of flexible membrane having a crescent-shaped posterior edge. In similar position in the floor of the mouth, just posterior to the symphysis of the mandibular bones, is a similar but larger breathing valve, whose hinder crescentic edge, however, swings free of the anterior end of the somewhat movable tongue. In this valve are marked depressions to receive the great premaxillary teeth. These valves may be plainly seen in figures 6, plate II; and 9 and 10, plate III.

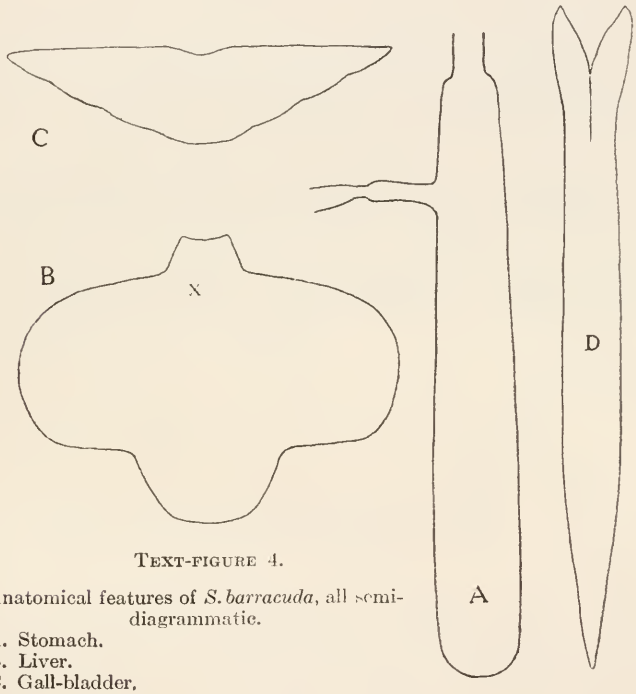
The action of these valves is very interesting. Ordinarily they lie horizontally, the one having above it and the other below it a space large enough for one to move about therein the handle of a scalpel, or, in a large specimen, one's finger. In gentle breathing, these valves swing slightly forward and downward for the one, forward and upward for the other. But in violent expiration, in consonance with the sharp upward rise of the floor of the mouth, the hyoid region, and the strong pulling together and downward of the gill-covers, the water would be forced forward out of the mouth but for these valves. Being elastic and markedly distensible, they swing together in a horizontal median line, catch and hold the forwardly moving column of water, which is then forced out backwardly over the gills and out under and behind the gill covers. With the relaxation of the hyoid region and opercula, the elasticity of the breathing valves brings them back to their normal horizontal position.

The reason why this fish has such well-developed breathing valves results from the fact that it does not close its mouth in expiration. This in turn is probably to be correlated with the extraordinary development of the great teeth, especially those on the anterior parts of the premaxillaries, since when the mouth is closed these must fit into the depressions in the anterior part of the mandibular valve. Because of these great teeth it is probably both more convenient and more comfortable for this fish to keep its mouth more or less open, even while breathing.

## INTERNAL ORGANS.

Of no less interest than the structures just described are the internal organs. Of fish No. 10 (3 feet 10 inches in extreme length) careful dissection and full notes were made. The abdominal cavity was 18.5 inches long from the diaphragm to the anus, with a 1-inch post-anal extension to be described later.

There seems to be in this fish a structure apart from the pericardial sac which functions as a true diaphragm. Cuvier and Valenciennes (1829) speak of a diaphragm in the European form, the spet. Contained in the body-cavity were the spermaries, the air-bladder, and the alimentary tract with the liver and spleen. The digestive apparatus was 29.5 inches long, of which the stomach was 12.5 inches long by 1.5 inches wide, and the intestine 17 inches long by 0.5 inches wide. The stomach had the shape shown in text-figure 4 A, the intestine coming off 2.5 inches below or behind the œsophageal constriction. The sac below the pyloric opening was filled with the bones of fishes. My notes say that this organ was supplied with three large blood-vessels, but their connections were not worked out.




TEXT-FIGURE 4.

Anatomical features of *S. barracuda*, all semi-diagrammatic.

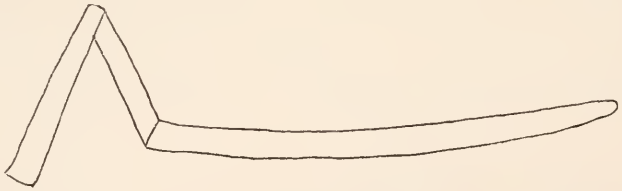
A. Stomach.
B. Liver.
C. Gall-bladder.
D. Air-bladder.

When the abdomen is opened the first organ visible in the anterior end is the liver. This is shaped very like a flat or English riding saddle turned upside down, the "skirts" or flaps extending upwards on each side of the stomach. It lies in the extreme forward end of the abdomen just behind the heart. In specimen No. 10 it was just about an inch thick at the forward end, where it was thickest (the point marked x in the diagram, text-figure 4B). On the dorsal surface, opposite the point marked x, the bile duct, 3.5 inches long, was given

off. This extended back to the gall bladder, which lay alongside the small intestine just anterior to the spleen. The gall bladder was 2 inches long and 0.5 inch wide, and was shaped somewhat like two conventionalized wings placed base to base, as shown in the diagrammatic figure 4c. The spleen had the same general shape, but was 3.25 inches long by 1 inch wide.

Lying between the body of the liver and the upturned "skirts" of the saddle (which were placed against the lateral walls of the abdomen) was the great mass of the pyloric cœca, which mass was shaped much like the liver, but had a greater volume and occupied a greater area. Of these cœca, only those lying on the dorsal and ventral surfaces of the mass were counted, but even these numbered 148. Dorsal to this mass of cœca were the stomach and small intestine.

The dorsal part of the abdominal cavity is occupied by the much-elongated air-bladder. Anteriorly this is bifurcated to form two horns, posteriorly there is but one which occupies the short post-anal extension of the abdomen (this was 1 inch long in a 3-foot 10-inch specimen). A fish 2 feet 10 inches in extreme length had an air-bladder 11.5 inches long, the anterior end of which had a 2.5-inch bifurcation. In a 3-foot 7-inch specimen, the air-bladder measured 15 inches, the horns being 3.5 inches in length. A third specimen, measuring 3 feet 10 inches between perpendiculars, had in its 18.5-inch abdominal cavity a 16.5-inch air-bladder, the bifurcation of which extended forward 3.5 inches. The general shape and appearance of this organ is shown in text-figure 4d.



Text-figure 5. Spinal column of a fish found embedded in mesentery of a barracuda.

While dissecting this fish, some hard object was found embedded in the mesentery. At first it was thought that it was a mummified pipefish, but when freed of all attached material it was seen to be the backbone of a fish. This was confirmed when a portion of it was put under a microscope. It was fairly straight save at the upper end, where it was bent as is shown in text-figure 5. It is hard to conjecture just how this vertebral column could have worked its way out through the wall of the intestine into the mesentery. Inclusions, while not common, are not unknown. Some half dozen or more have been noted, but will not be considered here.

The first of the old writers to give any account of the internal organs of a *Sphyræna* is Rondelet (1558). His brief statement concerning the spet of the Mediterranean is as follows: "It has a long stomach with several additions [cœca], the bowels are long, the liver whitish."

Sloane (1707) briefly says that its stomach is "sack-fashioned," and that the cœcal appendages are very many.

Parra (1787) makes no mention of the viscera other than the air-bladder. This in his specimen was 12 inches long by 5 inches thick. His figure of the air-bladder, while crude, is in the main correct.

Cuvier and Valenciennes (1829) give a very definite description of the internal organs of a fish of the species described by Rondelet:

"The viscera are simple, elongated. The liver has only one lobe, placed on the right side of the abdomen.

"The œsophagus is short and soon is transformed into the stomach, which is an elongated but narrow sac of such a kind that the capacity of the viscera is not very great. The pylorus opens close to the cardiac end near to the diaphragm; it is provided with a very great number of cœca, disposed in a single row on the length of the duodenum. The intestine is narrow and goes straight to the anus without making a bend."

They note that the liver is black, rather thick, rounded at its extremities, and placed across the middle of the stomach. The swim bladder is large with the upper walls thicker than those next the viscera. It is pointed behind, but forked in front. Each horn is pointed and terminates near the skull, but no communication with the auditory capsules could be found.

Of our form, *Sphyræna barracuda*, Cuvier and Valenciennes merely say that its viscera are very similar to those of the European form, the chief difference being that its stomach is larger.

Where so many other structures were found to be so markedly individual it was something of a disappointment to find the reproductive organs entirely normal in structure and position. They were, however, very large, befitting a fish of this size. No. 10 (3 feet 10 inches over all) was a male with a spermary bifurcated in front but coalesced behind into a common tube ending in the genital pore. The right lobe was 8, the left 9.5 inches in length anterior to the point of bifurcation.

The gross structure of the ovary is precisely that of the spermary. My largest specimen (No. 12) was a female 4 feet 7 inches long over all. The right lobe of her ovary was 14.5 inches long, at the left sac 15.5—the eggs being immature. This huge ovary was presented to the United States National Museum, to the authorities of which I am indebted for the beautiful photograph which forms figure 14 of plate IV.

In the course of this research the only reference found to the structure of the reproductive organs is in Cuvier and Valenciennes (1829), and they merely note that the spermaries and ovaries are two straight sacs found in the hinder part of the abdomen.

## HABITS.

Little is known about the habits of the barracuda, hence the few notes that have been collected in the course of this research may be of value. The fish seems in the main to be rather solitary. Only once was a school of them noticed. The water at Loggerhead Key being too shallow for an anchorage for our yacht, the *Anton Dohrn*, she was kept tied up to a buoy in the deep channel southeast of the sally-port of Fort Jefferson on Garden Key. Around the *Dohrn* thus anchored a small school of barracudas could sometimes be seen, and 6 or 8 fish were noticed on June 23, 1912. They were possibly attracted by the scraps thrown overboard from the galley; at any rate they were made bold by hunger, for, after one of them had been struck with the grains and wounded, another one of the school was taken on a trolling spoon thrown out and rapidly pulled in by hand. The appearance and attitudes of the members of this band are faithfully shown in Bullen's (1904) figure reproduced opposite page 55.

On one other occasion what may perhaps be described as a small school was seen. While trolling one day between Loggerhead and Bird Keys I had a heavy strike and, on hauling in, brought a large barracuda to the surface. Remarkable to say this had as a companion on either side a barracuda nearly as large as itself. These had their heads in the region of the right and left pectoral fins of the captive. For this no explanation can be offered. When the captive was brought nearer the boat, its companions disappeared.

The earliest reference to the fish called *Sphyræna* is in Aristotle's "History of Animals" (Book IX, chap. 3, 610*b*, 5), where it is listed among fishes that go in schools. Rondelet (1558), however, says nothing about such a habit, nor do Cuvier and Valenciennes (1829) refer to it, but they say of *S. guachancho* that "This species travels in companies, and there are sometimes taken together more than 200 individuals, all of the same size." Finally, Henderson (1916) speaks of the picudas or barracudas (maximum length 6 feet) ranging the water in schools or squadrons. Whether or not Cuvier and Valenciennes, and Henderson also, had in mind the subject of this paper, the great barracuda, can not, of course, be said. There are at least three species of the genus *Sphyræna* found in the West Indies, and all are commonly called barracudas.

In support of the present writer's contention that the big barracuda is solitary rather than social, Holder may be quoted (1903, p. 90; 1910, p. 125); and Holder has known this fish as no other scientific man ever has. This declaration of Holder's is concurred in by Bullen (1904), who says of the West Indian species that it is a morose and solitary fish, that even two are seldom seen together—in short that it seems to be a "comparatively scanty species." As to the California barracuda (*S. argentea*), Holder says that it "runs in schools, some of which have been seen miles in extent." And of the South Pacific

form, Bullen (1904), speaking of New Zealand waters, says that "In no other place have I seen the Barracouta swim in schools of hundreds of thousands, almost as closely packed as mackerel." Ward (1907) succinctly says that on the east coast of Australia it goes "in schools which rival those of the herring and mackerel for numbers and denseness." At Beaufort, North Carolina, the present writer has frequently taken as many as a dozen of the young of *S. borealis* at one haul of a 100-foot seine, and it may be that the *young* of the big barracuda go in schools.

However, so far as the present writer's experience goes, the large fish are rather solitary, and such individuals are frequently to be found lying motionless near the surface of the water around large coral heads reaching nearly to the surface, around buoys, channel stakes, wharves, wrecks, etc. One or more individuals could be found almost every day of the season of 1912 "hanging around" our western dock at Loggerhead. Three other kinds of fish had the same habit at the same place, *i. e.*, gars, gray snappers, and "minnows." The last two kinds plainly came to get fish scraps from dissections and débris thrown overboard by the cook and they were prompt in their attendance. The gars, and in large degree the snappers also, fed largely on the minnows, while the barracudas fed on all three indiscriminately. Considerable sport was had shooting these gars with a 22-caliber rifle, but after wounding or killing them none was ever secured, for the barracudas snapped them up at once. However, in turn these were often taken with baited hooks.

The big barracuda has the interesting habit of herding its prey either until it has digested its previous meal and again feels hungry or because, being thoroughly savage and bloodthirsty, it enjoys the game. Perhaps both conjectures are correct. A number of instances of this sort have been noted. On June 9, 1912, off the southern coal shed at Fort Jefferson, a 30-inch barracuda was observed to have a small school of gray snappers herded in shallow water. Although I went quite near them, they paid little attention to me but huddled close together and as a flock moved one way or the other as the barracuda moved. They seemed to be in abject fear of it and made no effort to break away until I scared it off. In the same afternoon a 4-foot barracuda was observed under our eastern dock at Loggerhead herding a big school of fishes comprising some 150 gray snappers 12 to 16 inches long, and numbers of yellowtails, grunts, parrot-fishes, angel-fishes, surgeon-fishes, cock-eye pilots, etc. These hung around the piles and swam among the rocks piled on the foundations of the dock to strengthen it, and not one of them dared make a break for liberty. A trolling spoon was procured and thrown out to the big fish, whereupon he slowly backed off into deeper water, and *then* the assembly broke up.

One other instance of like kind may be given. During the first two weeks of June 1913, a big barracuda laid off our eastern wharf, herding the gray snappers and making it unsafe to bathe. Almost daily efforts were made to hook him, and a pair of grains was kept on that dock for his special benefit, but he avoided grains and eschewed hooks and herded snappers, until possibly he became careless. At any rate Capt. Wm. Lee Wilson, finding him engrossed with the snappers, broke his back with the grains late one afternoon and brought him in alive and kicking. This fish was a male 4 feet 1 inch long and weighed 21 pounds, the largest specimen but one ever taken by us. It is interesting to note that a barracuda thus engaged in standing guard over a herd of fish in the manner just described, will nearly always be found to have its broad forked tail slowly waving from side to side, vibrating very like the tail of a cat watching a rat hole. This has also been noticed by Holder (1908).

Of the breeding habits, absolutely nothing is known. Judging from the habits of the fish it seems probable that the eggs are pelagic. Thompson (1905) says that he took specimens 1.5 inches long inside the little sheltered lagoon of Bush Key. Still earlier, Holder (1903) says that at Tortugas spawning occurs in the spring, but adds that very young fishes are rarely seen, although specimens 8 inches and upwards are not uncommon. At Beaufort, North Carolina, the writer has frequently taken in July the 1.5 to 5-inch young of the northern barracuda (*S. borealis*).

No young barracudas were caught at Tortugas during the summers spent there by the writer, but 4 little ones were taken in the summer of 1916. Concerning these, Professor Longley (with whom I have had the pleasure of studying the fishes of Tortugas) kindly writes that on July 14 one about an inch long was dipped up somewhere out in the open. This "was marked with a distinct lateral band of brown pigment running the length of the body through the eye." The three others were taken on the west side of Bush Key; one about an inch long from over grassy bottom, the others 1 to 2 inches long from over sandy bottom. Dr. Longley thinks that all were probably swimming near the surface. These were unfortunately not preserved, since it was not known then that I was at work on this fish.

As noted previously, four young of the great barracuda were taken at Tortugas during the summer of 1917. They vary from 2.25 to 2.6 inches in length to the base of the caudal. The total length can not be given, since these specimens came to me dried and in handling their brittle caudal fins have lost their points. These are believed to be the smallest specimens ever studied.

Since writing the above, some corroborative data has come to hand and its inclusion here will be of value. Weber in his "Fische der Siboga-Expedition" (1913), in commenting on the widespread distribution of

the Sphyrænidæ, says that this is probably due to the fact that the young stages are pelagic. He adds: "I captured in the sea far distant from the coast, in the surface plankton, a specimen only 13 mm. long of a Sphyræna species, which I have been unable to identify." He then adds that he has also taken four specimens of *S. jello* varying from 47 to 55 mm. long.

## HOW THE BARRACUDA MAY BE TAKEN.

Taking advantage of the habit of the barracuda in basking near the surface of the water, and of its insatiable curiosity, it was our custom to have a trolling-spoon behind the *Velella* or the *Henderson* (our smaller launches) on their trips to and from the various collecting-grounds. In this way most of the barracudas studied were caught. These spoons were connected by a swivel to a "snood" of 6 or 8 feet of piano wire, and this in turn by means of another swivel was attached to the heavy cotton hand line. The wire was necessary to keep the fish from cutting the line, and the swivels to keep it from snarling the latter while endeavoring to break away.

Our largest barracuda was thus taken in the summer of 1913. In the latter part of the season we secured several good specimens, but during the first part the barracudas took our spoons in one, two, three order until it seemed that every big barracuda in the harbor was thus decorated. Chief engineer John Mills, however, provided some extra strong tackle, and with it was caught the largest specimen ever recorded from the Tortugas. This was No. 12 of the table, a female 55 inches long and 38 pounds in weight. Some of the incidents of its capture will illustrate the strength and vigor of these powerful fish.

While trolling one afternoon there came a tremendous strike which nearly pulled me overboard. Responding vigorously, this giant barracuda rose some 2 or 3 feet in the air.* The *Velella* was slowed down and I began pulling the fish in hand over hand as rapidly as possible. Captain Wilson jumped into the glass-bottomed boat, which was towing behind, and began helping me, the fish offering a vigorous resistance all the time, leaping and backing, and dashing from side to side. Finally, when the line had been hauled in fairly short, the fish ran under the skiff, caught Captain Wilson amidships with the line and slewing the boat around nearly threw him overboard; and even when safely slid over the rail into the boat, it threshed and hammered around at such a rate that it was feared that it would break the plate glass bottom; nor did it become quiet until it was soundly trounced on the head with a monkey wrench.

In the matter of the capture of the barracuda I am happy in being able to add further data from a man who can speak with authority,

*In none of the books and articles consulted in this study of the barracuda have any accounts been found of leaping by this fish save only in Büttikofer's book (1890). He says that on the coast of Liberia, they often leap when in pursuit of smaller fish. My brother, while fishing among the Florida Keys, has had them leap when hooked.

for Charles Frederick Holder lived as boy and man for many years on the outer Florida reef and knew it and its fishes as no other scientific man ever has. Among these fishes, he had much acquaintance with the barracuda. During several years spent at Fort Jefferson on Garden Key, he had great sport with the barracudas in the lagoon. He used the hand-line (trolled) sometimes, but being in search of sport rather than specimens, for the most part he trolled with a rod and light tackle. He generally had a white rag tied to a string 4 or 5 feet long trolling behind the boat, as a lure to "flush the fish." When the fish was "flushed" he would cast out his bait, which he notes must be a fish with bright shining silvery sides, and was rarely disappointed in getting a strike. Holder makes it plain that the fish falls a victim to its own inquisitiveness; but when a large specimen is hooked, and if the angler uses light tackle, there is a battle royal before the fish can be gaffed. He writes very interestingly (1903) of the barracudas in the lagoon at Tortugas.

The earliest writer to speak of taking them by trolling is Dampier, in his "Two Voyages to Campeachy" (1729, 6th ed.): "We commonly take them when we are under Sail, with a Hook towing after our Stern." Labat (1742) also notes that they are taken with the line and adds "by the use of the seine" also, but is careful to say that these latter are only small ones, not over 3 feet long. However, the first reference found to the use of a lure is in Macgillivray's "Voyage of the Rattlesnake" (1852). He says that in Bass's Strait (between Australia and Tasmania) they took them with "a hook towing astern baited with a piece of red or white rag." Once at Tortugas our stock of trolling spoons having been depleted, successful use was made of a small steel shark hook to which a piece of white canvas had been attached.

Bullen (1904) gives numerous instances of catching barracudas by trolling in various seas, and also tells of catching them by still fishing. He gives an interesting account of how the Maoris of New Zealand catch their barracudas by a kind of fishing which might be called trolling. This method, which is only possible because the fish go in great schools, is so absolutely novel that it seems worthy of incorporation here:

"Take a stout rod, say 8 to 10 feet in length, or rather a pole, fairly rigid and tough, but not too heavy. To the end of it secure a piece of strong fishing line 5 or 6 feet in length. To the free end of this line attach a lure made as follows: A piece of red pine (*rimu*) 4 inches long, an inch wide, and half an inch thick, is scraped smooth and bright so that it will glow crimson when wet. Through one end of it is driven a 2-inch nail, which is carefully bent upward and filed sharp. Then this lure is fastened to the line in such a manner that, in case of the splitting of the wood, the fish shall not be lost. Now the boat, in which two fishermen sit to windward facing forward, is sailed briskly to and fro, the fishermen meanwhile whipping the water occasionally until a barracouta snaps at the bait and with a dexterous swing is flung into the boat, where, as there is no barb on the hook, he immediately

falls off. At the same time the peak halyards are let go, so that the boat's way is deadened and the fishermen ply their poles energetically. If they have struck a school, the fish rise and fall into the boat with rythmical regularity, every sweep of the bait into the water securing its fish."

The method, of attracting the fish by means of a lure and catching it by means of a spoon or a white rag on a hook, undoubtedly owes its success to the large inquisitiveness and utter fearlessness of the fish. To this desire to strike at anything flashing through the water, Bullen accredits the frequent loss of patent-log screw propellers, which are trailed behind vessels to give the rate of speed and register the distance traveled. This has been confirmed by Dr. A. G. Mayer in conversation with the present writer.

On rare occasions one of our laboratory men, all of whom were more or less expert with the grains, would "strike" a specimen. Thompson (1905) says this may be easily done; but we found the fish too wary for much success along this line unless its attention was distracted, as was the case of specimen No. 11 previously described.

Holder in another book (1908) gives an interesting account of how a boatman of his named "Barracuda" used to take the fish of the same name with the grains. Trolling a white rag behind his rowboat as a lure, he would scull the boat into the sun. In this way the fish would face the sun and be dazzled by it, while the striker would have his back to the luminary with everything behind the boat clearly illumined. When the fish was thus brought within range of the grains, the boat would be suddenly stopped, and as the fish, still watching the lure, would forge slightly ahead on one side, the grains would be thrown.

## FOOD AND FEEDING.

This fish is as strictly carnivorous as the shark, although hardly so indiscriminate in its choice of flesh. So far as my observations and dissections go, it is wholly a piscivore, feeding entirely upon other fishes. It is not meant to convey the idea that it will refuse other flesh food, but that left to itself its staple food is fish. In this I am happily corroborated by Linton (1910), who found in the stomachs of ten Tortugas specimens, collected in the summers of 1906, 1907, 1908, no other food than fishes.

With regard to the food of the big barracuda and the condition in which it is taken in, dissection of fish No. 12 (55 inches long) gave valuable data. Its stomach was enormously distended and, when opened, was found to contain some 5 pounds of fish in large fragments, surrounded with a lot of smaller fragments and topped off with the latter half of a fair-sized Margate grunt in a rather advanced stage of decomposition. The fish merely chops up its prey and swallows the large fragments whole.

Holder (1903) found that the barracuda could be taken only with a bait of shining-sided fish, and that it scorned all other baits, including

the much-vaunted and everywhere successfully used "crawfish." Probably the curiosity of the fish is attracted by the silver-sided fish as it is by a trolling white rag or spoon There is no evidence whatever that it at any time eats "crawfish," as the large spiny crustacean (*Palinurus*) of the reef is locally called.

Most writers on this fish say that it is carnivorous, but most of them are so obsessed with its apparent desire for human flesh that they refer to no other source of food. However, Cuvier and Valenciennes (1829) speak of a spet of the "middle sea" having its stomach filled with atherinas and little clupeids. Bullen (1904) dissected specimens from the Indian Ocean and found their stomachs filled with small mackerel. The man-eating habit referred to will be discussed in another section.

With regard to its piscivorous feeding habits, Bullen (1904) tells a story which is worthy of condensation and reproduction here. It seems that while the oceanic waters around New Zealand abound in fine food-fish, the fresh waters are almost totally devoid of fishes worth taking for either food or sport. Consequently, at great expense of money, time, and trouble, salmon eggs were sent out many years ago and planted in one of the rivers. Some of the eggs hatched, and some of the young survived. These grew apace and finally reached the stage when, following their natural instincts, they journeyed seaward. Down in the estuary of their river they first tasted the salt water, but here some native barracudas were prowling around in a school seeking what they might devour, and few if any of the young salmon ever went back to their place of birth. This story illustrates not merely the feeding habits and voracity of the barracuda, but the necessity of knowing the natural history of the native animals of a country before attempting acclimatization of new ones.

## PARASITES.

From what has been said as to the food and manner of feeding of the big barracuda, it is to be expected that it would be the host of all sorts of entozoa, parasitic helminth worms, but strange to say such is not the case. Having myself paid no attention to such parasites in my specimens, I have naturally turned to the writings of Professor Edwin Linton. Fortunately Professor Linton has spent considerable time at Tortugas studying its parasitic entozoa, and among the fishes examined were numerous specimens of *S. barracuda*. In 1908 he notes that 3 large and 4 small barracudas were examined, and in these immature nematodes were found for the most part encysted in the viscera. Likewise a few trematodes were found. So few were parasites of all kinds that Linton notes:

"It is perhaps worthy of remark that the great barracuda, which is a very voracious and predatory fish, appears to harbor but few parasites, either as a final or intermediate host. This conclusion is warranted also from the

results of the examination of five barracuda in Bermuda in 1903. The largest Tortugas specimen measured about 1.5 meters in length; the Bermuda specimens were about half that length. It would be of interest to know whether the apparent immunity from parasites of the barracuda and other fish is correlated in any way with the digestive ferments."

In his later paper dealing with the trematodes, Linton (1910) notes the examination of eight barracudas, in every one of which he found specimens of a new or at any rate undetermined species of *Gasterostomum*. This seems to have been the only parasitic trematode which he found in the barracuda.

However, an *Ascaris* has been found by Linstow (1906) in *Sphyranura barracuda* from Tasmania. Linstow's generic name is presumably a misspelling of *Sphyræna*. Other than the references given, no accounts of internal parasites of the barracuda have come to light. The fish seems singularly free from such unwelcome guests.

We now turn to an animal which in the past has been considered as an ectoparasite to its hosts, the barracuda included. I have among my notes gravely worded accounts of the finding, when the so-called parasites had been removed, of places worn in the skin or scales of the host; further it has been accused of living on the blood of its host thus obtained through the skin; and, most preposterous of all, one account specifically states that when one had been removed from the bottom of the boat to which it had adhered, the planking was found to be injured. Reference is made to the sucking-fish, *Echeneis naucrates*, for small forms of which the great barracuda sometimes acts as host.

On July 4, 1914, while trolling east of Loggerhead Key, the writer took a barracuda 40.8 inches long. When hauled in it was very active and called for strong repressive measures before it was quieted. When the *mêlée* was over there was found clinging to the deck the smallest example of *Echeneis* I had ever seen. This fish was about 4 inches long and had a most remarkable tail, plumose instead of crescent-shaped. It was carried to the laboratory and, as it seemed sick and the hour was late in the afternoon, it was put into an aquarium to be studied the next morning. When morning came it was gone and no trace of its whereabouts or its manner of going was ever found. Some two years later I was greatly interested to read in the "Memorias" of the Cuban ichthyologist, Poey (1856-58), the following description of a little *Echeneis* which he calls "*E. sphyrænarum*, the sucker of the Picudas."

"This little fish has never been found up to the present time save only on the *Sphyræna picuda*. It hides itself among its hosts' gills and escapes therefrom when the large fish is taken. The individual which I describe is 75 mm. long. In size [depth?] it scarcely exceeds a centimeter, since it is shrunken by concentrated alcohol and its body is greatly diminished. One sees, however, that its structures are all elongated. The eye is contained 5 times in the length of the head. The disk ends towards the [anterior]

third of the pectorals, and has on each side 10 lamellæ furnished with spines in one rank alternately long and short. The mouth is homodont: the teeth of the jaws and vomer are cardiform, but the lower jaw shows on the outside a peculiar character; it projects, is a little enlarged, ends squarely, and bears on each side toward the point an external row of five hooks (crochets), strong, and pointed, remarkable for their development. The pectorals arise near the opercles, and between their points and the origin of the vertical fins the distance is equal to the length of the head. The unpaired fins are opposite each other and have the ordinary form. They arise at an equal distance from the point of the snout and the end of the tail, the point not being considered. This point, formed of the two middle rays, is $1\frac{1}{2}$ times as long as the rest of the caudal, a character very distinctive of this species. The dried condition of my specimen forbids a count of the rays. The color is a very dark blue verging on black. The pectorals are white except at their bases. The two anterior points of the vertical fins are white, as are also the upper and lower edges of the caudal fin, but not the point which terminates it."

One other reference may be cited just here: Lütken, writing in 1878, speaks of an *Echeneis lineata*, a fish identical with Poey's *E. sphyræ-narum*, which he found among the collections in the museum of Copenhagen. This was taken in the South Atlantic from a *Sphyræna barracuda*. Lütken thinks that this particular Echeneis is to be found attached only to the sphyræna.

Mr. Peter B. Roberts, keeper of the fish market at Key West, Florida, has collected for me a considerable number of small specimens of *Echeneis*, ranging from about 4 to 7 or 8 inches long. I wrote him asking from what fish these were taken, and his answer was "that the sucker-fish are found on almost every fish in the waters around here, but the greater numbers are found on what are commonly called around here the amber-jack and the black grouper—that is, the smaller ones like you wanted collected."

I then wrote him that a certain small sucker-fish was thought to be found only on the big barracuda and asked for information on this particular point. Now, Mr. Roberts, by virtue of his position at Key West and his long experience both as fisherman and distributor of fishes, has an exceedingly wide and accurate knowledge of the fishes of that region. He writes:

"In answer to your questions I would like to state that the fishermen say that there is only one kind of [striped] sucker-fish, and that the small ones are not a distinct kind from the larger ones, but as they grow they naturally cling and stick to the larger fish. The ones found on the barracuda are the same as those found on other fish, the larger they grow the larger the fish they go after. . . . I would like to say . . . that I think that they are all the same kind, both big and small, simply growing through the different stages of life."

After the receipt of this letter the little suckers sent me by Mr. Roberts were carefully examined; 3 were found to have 19 lamellæ, 9 to have 20, 8 had 21, 6 were supplied with 22, 5 with 23, 1 with 24, and

2 had 25. The smallest had pointed tails, *i. e.*, had the central caudal rays longest and all had tails more or less plumose like that of the lost specimen above referred to. Presumably some of these were taken from barracudas. According to Jordan and Evermann they fall into the species *E. naucrates* (XXII to XXVIII lamellæ), or to *E. naucratoides* (XX to XXI lamellæ). At any rate, none of these can be identical with Poey's *E. sphyrænarum*, which had only 10 lamellæ. Gill (1862), in his criticism of Poey's identifications, calls this fish *Phthierichthys lineatus*, the striped louse-fish. Jordan and Evermann (1898) follow Gill, and note that this little sucker-fish is found attached to barracudas. This, however, is probably an echo of Poey. At any rate, the point as to whether or not the big barracuda is the sole host of this particular sucker-fish is worthy of further investigation.

## USE OF THE BARRACUDA AS FOOD AND POISONING RESULTING THEREFROM.

There is a long-standing prejudice against the use of *Sphyræna* as food. Salviani, the Roman physician and student of fishes, says in his book published at Rome in 1554, that "At Rome they are justly held to be common or cheap fish, nor do they have any proper fashion or mode of rendering them savory." Cuvier and Valenciennes, in referring to Salviani's statement, say that other writers, presumably contemporary, accord it a comparison with the haddock, everywhere esteemed as food; and that still others say that its flesh is light, friable, and of good flavor. Rondelet (1558) likewise testifies that its flesh is white and pleasant to the taste.

With regard to the use of the West Indian barracuda as food, there is likewise a widespread and long-standing prejudice based on centuries-old allegations of its poisonous qualities. This is such an interesting and important point that it will be taken up in detail and an effort made to get at the truth and its explanation. This belief, so far as the writer knows, was first noted by Du Tertre. He writes as early as 1667 that the flesh is like that of the pike, but dangerous to eat since it is sometimes poisonous. He then tells us that to determine whether it is hurtful it is necessary to examine the teeth and liver. If the former are white and the liver sweet-tasting, it may be eaten with impunity; but if the teeth are black or the liver bitter or harsh, it "ought no more be eaten than arsenic." As an explanation of the origin of the poison, he says that in the West Indies in his day it was thought to be due to the fact that the fish eats the fruits of the very poisonous manchineel tree which have fallen in the water. That this explanation has persisted we will see later. And since this explanation of the poisonous quality of the flesh of the barracuda is repeatedly offered, the following interesting corroboratory note seems worth giving.

Dampier (1729) in his first voyage to Campeachy landed on the Isle of Pines on the south side of Cuba near the west end. Among the animals of which he makes mention are large land crabs. Of their feeding he says:

"The Manchaniel Fruit, which neither Bird nor Beast will taste, is greedily devoured by them, without doing them any harm. Yet these very crabs that feed on Manchaniel, are venomous both to Man and Beast that feeds on them, though the others are very good Meat."

There is now to be quoted an account which, because no certain fish is named, may seem of doubtful relevancy, but which, as the sequel will show, is of direct value to the matter in hand, and in all probability relates to the very fish under consideration. In the Philosophical Transactions of the Royal Society for 1675 there is published an extract from a letter of one Mr. "J. L." to the publisher concerning poisonous fish in the Bahamas. It reads as follows:

"The Fish that are here, are many of them poysonous, bringing a great pain in their joynts who eat them, which continues for some short time, and at last with two or three days itching the pain is rubbed off. Those of the same species, size, shapes, colour, and taste are one of them poyson, the other not in the least hurtful. And those that are, are so only to *some* of the company. The distemper to Men never, that we hear of, proves mortal. Doggs and Cats sometimes eat their last. In men who have once had the disease, upon the first eating of the fish, though it be those that are wholesome, the poisonous ferment in their body is revived thereby, and their pain increased."

There is another account, nearly 200 years later, from the pen of the English surgeon, Morton (1868). Commenting on the great variety of fish caught at Nassau, he adds:

"Some of these fish, at certain times of the year, are very unwholesome, and, when eaten, give rise to severe purgings, vomiting, and cramps. During our stay, four men belonging to a coasting vessel were poisoned, one of whom died from eating part of a large barracouta, which they had caught. This fish, when large, is said to be very unsafe food, and great risk is run in eating it. The one which gave rise to fatal results in this instance, was upwards of five feet in length."

Sir Hans Sloane (1707), in volume II of his "Natural History of Jamaica," says of the barracuda:

"According to its feeding on venemous or non-venemous Food, 'tis wholesome or poysonous to those who eat it; 'tis also noxious in some Seasons of the Year, and in some Places, and innocent in others, I suppose according to its Nourishment, by which now and then, it acquires so much poison as to kill immediately."

However, Dr. Patrick Browne (1756) says, of the two species which he found in Jamaican waters, that "they are both firm and palatable fishes, much esteemed by many people."

Dampier (1729), in his "Second Voyage to Campeachy," thus speaks of the edibility of the barracuda:

"They are firm well-tasted Fish; but 'tis dangerous eating them, for some Men have been poisoned with them. Divers Persons are of the Opinion that these Creatures are poysonous in some Places only, and that but at some Times of the Year. I know that in many parts of the West-Indies, some have been injured by eating them, and that at different Seasons of the Year; therefore Seamen commonly taste the Liver before they venture any further; and if that has a biting Taste like Pepper, they esteem the Fish unwholesome, but if not they eat it: and yet I found even this Rule to fail too. I judge the Head and the Parts near it, to be chiefly venemous."

Labat (1742) discourses at length upon the edibility of the barracuda, whose flesh he says is white, firm, rather oily, and almost of the same taste as that of the pike, but at times is poisonous. He offers a very interesting explanation:

"As it is extremely voracious, it eats greedily everything which it finds within and on the water, it happens very often that it encounters *Galeres* [sea-nettles, medusæ, "Portuguese Men of War"] or the fruit of the manchineel, both of which are very violent and caustic poisons. The Becune does not die because it has eaten them, but its flesh contracts the poison and causes death in those who eat it just as if they had eaten the dangerous fruit or the *Galeres*."

To tell whether the flesh is good or dangerous, Labat would inspect the teeth. If they are black it is dangerous; if some are white and some black, then taste the liver. If it is bitter, reject the fish.

Catesby (1754) writing of the Bahama barracuda gives some details not found in any earlier writer. He evidently wrote of large specimens, for he says:

"The flesh has a very rank and disagreeable favour [flavour?] both to the nose and palate, and is frequently poisonous, causing great sickness, vomiting, and intolerable pains in the head, with loss of hair and nails; yet the hungry Bahamians frequently repast on their unwholesome carcasses."

Fermin (1769) says that the *becune* has firm, white flesh, somewhat oily, but of very good taste. However, it is not to be eaten save after taking the precautions noted above. He explains the poisonous properties of its flesh by its voracious feeding habits, especially by its feeding on the manchineel.

In 1808 a Dr. Chisholm published an article on the poison of fish. His observations were made while a resident of the island of Grenada, where he appears to have practiced medicine. He knew of and probably treated cases of poisoning resulting from eating the barracuda. He says that the fishermen account for this poison by alleging that the fish are poisonous only at the spawning season when they repair to and feed upon "sea-moss" [which Chisholm identifies as *Corallina opuntia*]. This poisons them and they in turn poison those who eat

it. After their return from the banks, the poison gradually leaves them and they become wholesome again.

Chisholm notes that copper is supposed to be the essential basis of this poison, but adds that he knows of "no facts which decidedly prove this." As to the value of salt as a preventive he says:

> "A barracuda, the poisonous quality of which was proved by its entrails killing a cat which had ate of them, being cut into slices or junks, and slightly salted or corned, was rendered perfectly wholesome, and, as usual delicious to the taste. Instances have occurred, however, in which salt has not exhibited its counteracting power."

Moreau de Jonnes, as early as 1819, and 1821, made extensive and intensive studies of poisoning resulting from eating fishes, the barracuda among others. In his later and fuller paper, he quotes various authors that crabs which eat the fruit of the manchineel become poisonous (thus confirming that very accurate observer, William Dampier), while those which have no access to this fruit are wholesome. He then takes up and disposes of the alleged causes of the poisonous quality of the flesh of certain fishes. He states that the first cause commonly assigned is that the fishes eat poisonous zoophytes. This he rejects because poisonous fish are found where these are absent and wholesome fish where they abound, because the same fish where these abound are not poisonous throughout the year, and lastly because he fed poisonous hydroids of all kinds to fishes and then fed these fishes to various animals and to man with impunity. The second reason adduced is that the fishes are poisoned by copper. Moreau de Jonnes, however, notes that copper is present and fishes wholesome on the English coast and that copper is absent and fishes poisonous in the West Indies, and finally that oysters grow on the copper bottoms of vessels and have been found wholesome when eaten. Then he takes up the manchineel theory. He notes that no one has ever proved that fishes eat the manchineel fruit, and that he has made many dissections of poisonous fishes (barracudas among them) without ever having found fragments of the manchineel fruit in them. He thinks that the eaters would be killed by the eating, and that, since these trees abound widely on seashores, there should be many more poisonous fish and crabs than there are. Finally, for himself he concludes that poisoning from eating fishes (barracudas included) is due to the fact that the flesh has some inherent poisonous properties, or develops such morbid qualities as a result of the hot climate. While our author gives the former explanation his very strong belief, we have in the second a premonition of the ptomaine theory.

Another physician, William Ferguson, writing some years later (1823), declares that the size of the fish has nothing to do with its poisonous qualities, nor does the use of salt destroy its noxious properties. Then he refers to a report from a physician in Martinique

concerning a family which had been poisoned by eating a barracuda which had lain in salt 24 hours.

The most extensive and possibly the most interesting account of poisoning by the barracuda is given by Cuvier and Valenciennes (1829) in their treatment of *Sphyræna barracuda*. The M. Plée quoted seems to have been a French naturalist who lived in the West Indies. Apparently his manuscript was sent directly to Cuvier, who writes in the first person:

"All that has been reported concerning poisonous fishes of warm countries and that malady called Siguatera, which is found under certain circumstances, has the power of inspiring curiosity and interest, so that I have thought I ought to insert here the data collected by M. Plée on the barracuda, just as I have found it among the papers of that unfortunate naturalist.

"'Some persons,' said he, 'fear to eat this fish, because it has been frequently proved that it is the cause of illness and sometimes of death. This poisonous property of the becune is present very certainly in a particular state of the individual fish, which appears to show itself at different seasons of the year.

"'I have consulted several persons with regard to the poison of the becune and all have assured me that there is an infallible means of satisfying one's self when one comes from fishing for it whether or not it is poisonous. He has only to note in cutting it whether or not there runs away a kind of whitish water, or rather a kind of *sanie* [*i. e.*, serum or exudation], which in all cases is a sure sign that the becune is in the diseased condition of which I have spoken above. D. Arthur O'Neill, Marquis del Norte, has told me that he has often made experiments on dogs and that all these have confirmed the sureness of this means of safety.

"'The signs of poisoning by the becune are a general trembling, nausea, vomiting, sharp pains, particularly in the joints of the arms and hands. Sometimes these symptoms follow each other so rapidly that it becomes extremely difficult to determine in a precise fashion the different stages of this deadly affection.

"'If death does not put an end to this malady, as happily is most ordinarily the case, one may sometimes see how the virus always causes certain singular pathological phenomena. The nails of the hands and feet gradually die and drop off; the hairs, which, as is well known, are of the same nature as the nails, finally drop out also. These phenomena have been noted in several individuals to have continued for a considerable number of years. One case may be cited in which this experience persisted for more than twenty-five years.

"'One remarkable fact is that when the becune has been salted it never causes any trouble. At St. Croix for instance, it is the custom not to eat it until the day following the one on which it was salted. May it not be that the salt is an antidote for the poison of the becune?'"

However, M. Plée adds in honesty that which spoils an apparently straightforward piece of testimony by saying that he has never seen a case of barracuda poisoning, but has had his information from persons "well instructed and worthy of confidence."

Widespread is the belief that this reported poisonous affection of the flesh is due to the fish's feeding on substances containing copper, as referred to in Chisholm's account. Gosse (1851) refers to the same

thing when he says that "the colonists believe [that it] is owing to its feeding on submerged 'copper-banks.'"

Poey (1856–58) writes that its flesh is excellent, but is forbidden to be sold in the markets because it is sometimes dangerous, and gravely affects the health of those who eat it at such times. The poisoning caused by fish is called *Ciguatera* and the best antidote for it is the juice of the citron. He then adds that such poisonings are rare but serious when they do happen, especially when caused by eating the picuda. Last of all he naively concludes that "One may eat it with full security if one will in advance try it on a cat." He adds that it is the belief of the fishermen that the fish is unsuitable for food if the roots of its teeth are blackish, but that he has no first-hand knowledge of the matter.

Duméril (1867) has gone very thoroughly into the matter of poisoning from eating fishes. He quotes a Dr. Court, a practitioner on the island of Trinidad, that the smaller barracuda species is harmless, as are small individuals of any fish held to be poisonous. The great sphyræna is often very poisonous. In addition to the teeth-liver tests, a new one is here given:

> "When a silver spoon or coin, placed in the vessel in which the fish is being cooked, does not become blackened, the flesh may be eaten without fear."

Duméril takes no stock in the copper-bed theory, but does suggest another cause for the poisoning. A Dr. Guyon, "sanitary inspector of troops at Martinique," communicated to Duméril some considerable data and: "According to him the real cause is a commencement of decay in the flesh of the fish" [accompanied by a giving off of $H_2S$ as shown by the silver coin test of the preceding paragraph]; and Duméril adds: "This opinion I also share." Here we have the first definite statement for our fish of what later has come to be known as the ptomaine theory of fish poisoning.

The prejudice against this fish seems to exist to-day throughout the West Indies. It is, however, a good food-fish. In our mess at the station we frequently ate *S. barracuda*. The small forms 18 to 20 inches or thereabouts, were excellent. Fish No. 3 of the table (page 58), 30.5 inches long, was pronounced by the mess to have a good flavor, somewhat like that of a flounder. Larger and older fish are likely to have coarse flesh, rather oily, and a somewhat characteristic odor. Such were used only for shark bait.

Temminck and Schlegel (1850) say that *Sphyræna obtusata* was fished for in the bay of Nagasaki, Japan, where it was regarded as a delicious food by the Japanese. While for *S. guachancho*, Guichenot (1853) quotes Ramon de la Sagra that its flesh is savory and excellent for the table, and unlike that of the becuna, is never poisonous and hence may be eaten without danger of Ciguatera. Day (1865) adds similar testimony for the Indian form, *S. jello*, when he says that it is sometimes eaten by Europeans though not particularly esteemed.

Büttikofer (1890) says the same for this fish in Liberia.

In his "Introduction to the study of fishes" (1880), Gunther notes that barracudas are commonly used as food, but sometimes (particularly in the West Indies) their flesh manifests poisonous qualities due to their having preyed on poisonous fishes; but as to the South Seas form (probably *S. commersonii*) he apparently quotes Andrew Garrett (1877), that it is freely eaten and highly valued as a food-fish.

Saville-Kent (1893), writing of this same form, affirms that in eastern Australia it is much esteemed as a food-fish. Macgillivray (1852) bears similar testimony for the Australian barracuda.

Bullen (1904) says that he has eaten the barracuda in the West Indies, around New Zealand, at the Cape of Good Hope and elsewhere, and has always found it a palatable food-fish. It seems to be especially prized for this purpose in Australia and New Zealand. In this, Ward (1907) is in hearty agreement. The California species, it may be noted in passing, is also excellent for the table.

In this connection Jordan (1905, II, p. 223) notes that the flesh of larger forms is often difficult of digestion and when eaten frequently results in serious illness. Of smaller specimens "The flesh is firm, delicate, and excellent in flavor." In the first volume of the same work (A guide to the study of fishes), Jordan discusses in very illuminating fashion the various forms of poisoning due to eating fishes. Quoting from Dr. Jacques Pellegrin, he says:

> "The flesh of fishes soon undergoes decomposition in hot climates. The consumption of decayed fish may produce serious disorders, usually with symptoms of diarrhœa or eruptions of the skin. There is in this case no specific poison, but the formation of leucomaines [ptomaines?] through the influence of bacteria. . . . It is especially severe in certain very oily fishes, as . . . [the barracuda]. The flesh of these and other fishes occasionally produces similar disorders through mere indigestion. In this case the flesh undergoes decay in the stomach."

I have not been able to find Pellegrin's paper (Les Poissons Vénéneux, Paris, 1899), but the abstract of it in "Revue Scientifique" for the following year contains for the barracudas the mere statement that the poisonous qualities of the flesh of these fish have an origin very difficult to establish.

In a recent bulletin of the New York Zoological Society (Nov. 1916) Mr. L. L. Mowbray examines with some care the matter of fish poisoning, which he calls "Ichthyotoxismus." Mr. Mowbray is an experienced collector of fishes for the New York Aquarium and has operated for many years in the Bermudas, Bahamas, and Florida Keys, particularly around Key West. He has studied at some length in all three localities the question of poisoning following the eating of fishes, particularly the barracuda, and has come to the conclusion that it is simply ptomaine poisoning. Mr. Mowbray's data are so definite, so much to

the point, and tally in so many points with the reports quoted above, that it will help clear up the matter to quote him in full. He writes:

"While in the Turk's Islands I questioned many fishermen concerning the fishes that were poisonous, the effects of the poison, and at what seasons the fish were most dangerous. Without exception their reports tallied. All agreed that there were two forms of the disease; that the fish from the north side of the Islands were the most dangerous, those from the south side not being so likely to prove poisonous. This seems incredible, as the island of Grand Turk, most densely populated of this group of islands, is only 1.5 miles wide by 6 miles long, and lies in the trade winds and the Bahama Current, which move all surface food at a considerable rate to the westward. I consulted Dr. Geogaghan, then the medical officer of the colony, who kindly gave me a description of the symptoms, which he had personally experienced in both forms of the disease. Dr. Geogaghan said:

"'To my knowledge the common poisonous fish are barracuda, jack, and muletto kingfish. In certain places, for some reason or other, the barracuda is more likely to be poisonous than if caught elsewhere. There are two distinct kinds of poisoning from these fishes. The ordinary type is similar to ptomaine, being in the nature of a simple gastro-enteritis of an irritative sort. It is characterized by acute spasmodic pain in the stomach, diarrhea, and vomiting, coming on from 10 to 20 hours after eating the fish, and subsiding readily under treatment. There is occasionally headache, usually fever (101° to 102° F.) and a rapid pulse (90 to 100). Generally speaking, it is an acute gastro-enteritis.

" 'The other form is in the nature of a toxemia. I have never seen a case following on the eating of jack, but can not be certain on this point. The symptoms are slow to subside, sometimes lasting for months. It starts from 2 to 6 days after eating the fish, very seldom less than 2, and usually 3 or 4. There is repeated pain of a dull resistant type over the region of the pancreas; constipation; slow aching pains in the joints, especially in the knees and back, without any physical signs; pain behind the eyes and headache, acute irritation of the bladder with frequent burning and tickling sensation.

" 'The joint pains are called "bone-pains" here, and are similar to the pains of influenza, though more particularly associated with the joints. There is an intense feeling of lassitude and debility, and subnormal temperature.

" 'Naturally clinical cases vary in severity. Occasionally the two forms of poisoning are combined, one following the other. I look on the first as a simple irritative disturbance of the intestine which throws off the irritant in the usual way. The second is a real poisoning of the system. I have had both myself and it was many months before I was rid of the joint-pains of the second.'

"The Turk Island species described herein are also among the principal food-fishes of Key West and the Bermudas, excepting the kingfish, which is seldom taken at Bermuda, and poisoning is unknown in these localities.

"After observing the conditions and the manner in which the fish are handled, I have reached the conclusion that the reason they are poisonous in one region and not in another, is that in Bermuda and Key West almost all fishing boats have live-wells, and therefore usually bring their fish to market alive, while in the Turk Islands and Bahamas the fish are killed and allowed to remain in the sun until the shore is reached—sometimes 5 or 6 hours after they are caught.

"All of the fishes considered poisonous are of soft flesh and rich in gastric juices, and are therefore the most likely to decay quickly; and, when eaten in a partially decayed condition cause *ptomaine poisoning.* Naturally some

are more poisonous than others. Those caught in the mornings are exposed to the sun's rays much longer, and are therefore much more decomposed.

"The fishes, when examined externally and internally, appeared to be in the finest condition when caught, and I could detect no difference between them and those of Bermuda or Key West. I have seen specimens at Grand Turk Island with the scales standing almost on edge through the decomposing of the flesh, which, forming gases, expanded the fish. These fish are frequently sold from house to house, though caught the day before and in a half-putrid condition. It is probable that if, when caught, the fish were eviscerated and bled, a case of poisoning would be a rarity.

"An interesting antidote for fish poisoning is used by the natives. When a fish has been eaten that is suspected to have been poisonous, the bones are saved for 24 hours, within which time, if at all, symptoms should appear. On the first indication of trouble, the bones are roasted, pulverized, and made into tea for the patient. Belief in the efficacy of this treatment is implicit, provided the bones of the right fish have been used."

In order to get at present-day notions at Key West, I again called on Mr. Peter Roberts for information and he very kindly wrote me as follows:

"As to the barracudas, it is not a certain time of the year that they are poisonous, but it is those of a certain kind that are poisonous. The only barracudas eaten around here are the ones caught along the shore and in shallow water. The barracudas that are poisonous are the ones that are caught in the Gulf Stream, and the people around here are very careful not to eat any of them. They are of a distinct kind, known as the 'Blue Backs,' and can be readily distinguished from the non-poisonous kind."

In this connection it is of interest to note that the beautiful colored figure of *Sphyræna barracuda* in Cuvier and Valenciennes (reproduced herein as figure 18, plate v) (1829) is yellow on the sides below the lateral line and on the fins and tail, while the back is a beautiful *blue*, the blue of the deep blue sky, almost as blue as deep sea-water. Furthermore my notes record that specimen No. 10 of the table, on page 58, had a blue sheen on the dorsum in certain lights.

Captain W. L. Wilson, previously referred to as one of our boatmen at Tortugas, was born and reared in the Bahamas. I wrote to him at Nassau about this matter and he replied:

"The old and large barracudas are, as a rule, poisonous. I have never known or heard of one under 3 feet being poisonous. After the fish are cooked you can tell if they are poisonous by taking a piece of the cooked fish and breaking it apart. If you find very small dark veins the fish is all right, but if there are no dark veins found it is poisonous."

The latest information on barracuda poisoning is from the pen of Stephen Haweis (1917) in his book on the sea gardens of Nassau, Bahamas. It seems to be solidly a quotation from the distinguished English ichthyologist, C. Tate Regan, the original of which I have been unable to locate. This statement is as follows.

"The largest of these species (*Sphyræna barracuda* or *picuda*) is a valuable food-fish, but it has long been known that individual specimens may be poisonous, causing severe illness and even death. There is evidently something more in this than ptomaine poisoning due to eating fish that is not fresh and the probability is that the poisonous quality of the flesh is not directly caused by the barracuda feeding in certain places or on smaller poisonous fish. It seems more likely that barracuda are poisonous when suffering from an infectious disease. Plée has stated that when barracuda are poisonous this can be recognized by a thin white fluid running out of the flesh when it is cut, whilst Poey says that the poisonous barracuda have the teeth blackish at the roots. However, no real investigation of the matter on scientific lines has been made, and it is quite likely that were such investigation made, the cause might prove to be quite different from what has been supposed."

None of the encyclopedias, not even the eleventh edition of the Britannica, contains the word "ciguatera." Parra (1787) has a short chapter bearing the heading "Ciguatera." This has been carefully translated for me, but nowhere does it contain any reference to the barracuda. Parra gives at some length and in very clear and minute detail an instance of ciguatera poisoning of himself and his family. This agrees in general with the accounts given above. He refers to the manchineel theory, but thinks it of no value since in certain parts of the West Indies where these trees abound the disease is wholly absent. He confesses himself entirely in the dark as to the cause and also the best treatment, lemon juice being the thing which affords some and possibly the most relief.

We have here some exceedingly interesting accounts of barracuda poisoning and some equally interesting if divergent theories in explanation. The present writer having had no personal experience or observation of it can not express any personal opinion. The flesh of the larger fish is coarse and oily and has neither appetizing appearance nor odor. Such flesh might well be provocative of gastric disturbances if eaten. With us at Tortugas such was used only for shark bait. Again it is quite possible that certain species might be poisonous on account of their feeding habits, and an even more plausible supposition is that these fish may be poisonous at certain seasons only of the year. As for the first it is well known that certain species in a group are poisonous while others are not. This finds explanation in the fact that certain poisonous alkaloids are found concentrated in some organ. These are most apt to be found in the ovary, and are most abundant and dangerous at the breeding season.

In the second place, it might well be that the barracuda, being a piscivore, might feed at certain seasons of the year on fishes which at that time were poisonous, and thus itself become poisonous. This might also lead to its being poisonous in certain localities only.

However, whatever other causes may give rise to barracuda poisoning, there can be no doubt that decomposition products, ptomaines,

formed by the action of saprophytic bacteria, must be reckoned with. These bacteria, as Fischel (1892) states, might be present in the flesh or blood, as such or as spores, or might get into the flesh through wounds and bruises, or by the intake of infected food. However this may be, fish (especially such as have oily flesh like the barracuda) "go bad" quickly under the tropical sun and when eaten in such condition would give rise to ptomaine poisoning.

## SIZE.

The big barracuda justifies its colloquial name by growing to great size. My largest specimen was 4 feet 7 inches long and weighed 38 pounds. This is the largest specimen recorded from the lagoon at Tortugas. However, one day I saw, under the wharf-house at Garden Key, a specimen that looked to be fully 5 feet long. As the *Velella* pulled out, I threw my "spoon" overboard, knowing that the fish would probably follow the boat, and hoping to get a strike. My hopes were realized, for before we had gone a hundred yards I had a strike which in 10 seconds left me with only a hundred feet of line and a groove burned in my right fore-finger just the size and depth of the line. The fish, with the spoon and remainder of the line, was not seen again.

Vincent, in his interesting, "Sea fish of Trinidad" (1910) speaks of somewhat similar experiences with blistered hands while trolling for what he calls the "pirate of the seas." But this is not unexpected when we read that his largest specimen measured 8.5 feet.

At Miami, Florida, on visiting a local taxidermist's shop, I found its walls almost lined with the mounted skins of big fellows 4 to 6 feet in length. These were taken on the Florida Reef some 6 or 8 miles away. Jordan and Evermann assign 6 feet as the average maximum size for the West Indian specimens, and this is corroborated by Henderson (1912), while Poey (1856) states that the Havana fishermen say that it sometimes attains a weight of "fifty livres" which would indicate a length of over 6 feet. As noted above, Holder has had wide experience with these fish and he states (1903) that he has taken them in the Florida Keys between 6 and 7 feet long and weighing 60 to 70 pounds. However, he adds that he has heard of specimens even larger than these.

One of the older writers on the natural history of the Antilles, Rochefort (1665), gives the length of the barracuda as from 6 to 8 feet with a girth in proportion. Du Tertre (1667) quotes Rochefort with approval, but gives no figures of his own. Sloane (1707) had only small specimens, but indicates that it grew to a large size. Labat (1742), however, makes up for any deficiencies by declaring that "They have been seen in this river [Gallion] 18 to 20 feet long and of the size of a horse." His statement, however, must be taken *cum grano salis*. Catesby (1754), speaking of Bahama fish, is more moderate, though his

figures come close to Labat's: "This fish grows to a large size; some of them I have seen 10 feet in length, and some I was told are much larger; though the more common length is that of about 6 or 8 feet." However, for present-day Bahama fish, Captain Wilson, who has seen hundreds, writes me that the largest measured 6.5 feet. But, Fermin (1769), writing a few years after Catesby, says that along the coasts of Surinam they were occasionally taken approximately 15 feet in length. These were certainly giants.

A photograph was made of the 55-inch specimen (38 pounds), but the photographer in developing the plate unfortunately broke it. Figure 1, plate I, is a photograph of a medium specimen which, however, contrasts well in size with the 11-year-old boy standing beside it. These fish, however, were small compared to the one figured by Wood-Jones. (See figure 2, plate I, of this paper.) Saville-Kent (1893) does not portray the Australian form, but notes that it sometimes attains a weight of 50 pounds, from which one may judge that such would be between 6 and 7 feet long. Günther (1877) quotes Andrew Garrett that the Polynesian form (probably *S. commersonii*) grows to 8 feet in length and 40 pounds in weight. This must be a very slender fish, as is the California *S. argentea* (maximum length 5 feet). However, the form found on the west coast of Africa grows larger. Büttikofer measured a *S. jello*, caught in the mouth of Cape Mount River, Liberia, which was 10 feet long.

However much the authorities may vary in their estimates of the size of the barracuda, all agree that that size is *great*, though it does not have the bulk of the jewfish nor that of some of the great groupers, and when along with its size consideration is given to its remarkable swiftness and its implacable temper, it must be acknowledged (the sharks alone possibly excepted) as the real ruler of the Gulf-Caribbean waters.

## THE BARRACUDA DANGEROUS TO MAN.

All the various recitals above will lead the reader to ask if this fish is not dangerous to man. The answer is that in southern Florida it is more feared than the shark. If the reader will now turn to figures 7, 8, 9, and 10, plate III, showing the teeth, and to pages 62 and 63, on which the formidable dental armature of this fish is described, he will find abundant reason for the dread generally had for this ferocious fish. But he needs to be informed of the utter fearlessness of the fish, of its ferocity, and of its insatiable curiosity.

The ordinary shark is usually an arrant coward. If a shark is "hanging around" a boat or wharf, and a man falls overboard or any large object is thrown overboard, generally that shark will depart in a panic. One day, when we were cruising around off the municipal slaughter-house at Key West, where there were some half dozen 10-

foot tiger sharks (*Galeocerdo tigrinus*) swimming around just out of harpooning distance, I questioned one of the most experienced of Key West fishermen (then in my employ) as to the danger of falling overboard in such a locality. He replied that there was practically none, and when, to draw him out, I professed to disbelieve him he coolly offered to prove the matter by jumping overboard *on* one of the sharks if I would steer him up close enough. So confident was I of the accuracy of his statements that, had the sharks not been wanted for specimens, I would have taken him at his word. Similarly the paddling and splashing of a number of swimmers will ordinarily drive off any shark. It must, however, be borne in mind that I am speaking of my experience and observations at Beaufort, North Carolina, and in southern Florida only. For an incident illustrative of this character of shark at Beaufort, see the account given by the present writer in 1912. But it is not thus with the big barracuda. He is inquisitive, utterly fearless, and seemingly of implacable temper. The Key West fishermen dread this fish much more than they do the ordinary shark. The whole matter was admirably put 250 years ago by the Sieur de Rochefort (1665) in his "Natural history of the Antilles":

"Among the monsters greedy and desirous of human flesh, which are found on the coasts of the islands, the Becune is one of the most formidable. It is a fish which has the figure of a pike, and which grows to six or eight feet in length and has a girth in proportion. When it has perceived its prey, it launches itself in fury, like a blood-thirsty dog, at the men whom it has perceived in the water. Furthermore it is able to carry away a part of that which it has been able to catch, and its teeth have so much venom that its smallest bite becomes mortal if one does not have recourse at that very instant to some powerful remedy in order to abate and turn aside the force of this poison."

One of the points above noted is expressly corroborated by Fermin (1769), who says in so many words that with its long trenchant teeth it is able to cut clear through and carry off anything which it encounters in swimming—a statement which may well be believed.

The other points in Rochefort's accounts are confirmed by Du Tertre (1667), who tells us that:

"This fish [which grows to a length of 8 feet] is greedy, blood-thirsty, bold, and is more dangerous than the Requiem [shark] . . . , because besides the fact that it can bite more easily, it is not startled by any noise any more than by the movements which may be made in the water. On the other hand, in order to investigate these, it launches itself at the persons [making these movements] in order to devour them."

Sir Hans Sloane (1707) gives some particulars of especial interest when taken in connection with other accounts to follow later:

"It is very voracious, and feeds on Blacks, Dogs, and Horses, rather than on White men, when they can come at them in the water."

This is concurred in by that keen observer, William Dampier. In his "Two voyages to Campeachy," which appeared in sixth edition in 1729, he says of "Parricootas," which he describes as long fish, having round bodies, and long mouths with sharp teeth, that:

"They commonly haunt in Lagunes among Islands, or in the Sea near the Shore. They are a floating Fish, and greedily take the Hook, and will snap at Men too in the Water."

To Pere Labat (1742), of the 18 or 20-foot barracudas, we owe some interesting data and even more interesting conjectures. On the question of its danger to man he writes:

"As it is not obliged to turn on its side like the shark when it wishes to bite, it is infinitely more dangerous. Our savages, who attack and kill Requins [sharks] and Pantoufliers [hammerhead sharks] with knives, do not dare to run that risk with Becunes, because, moving with such extraordinary speed, they carry away an arm, a leg, or a head as if they had been cut off with a blow of a sabre. It has happened several times that horses and other animals crossing [the river Gallion] by swimming have had their legs cut off or half their bellies carried away."

Going further into the matter, he writes:

"One is assured by many experiences that voracious fishes like the Requin, the Pantouflier or Zygæna, and the Becune attack more often a dog or a horse rather than a man, and a negro rather than a white man, when by reason of the overturning of a boat or canoe they find these different species of animals in the sea. I leave it to the curious to seek the reason, it suffices that that which I report is a veritable fact and testified to by those who have accurate knowledge of America and of other regions where these carnivorous fishes are found. My notion is that the bodies of dogs and horses give off 'corpuscles' which strike the fishes more strongly and attract them longer. Just as we see that wolves, crows, and even dogs more often come to carrion or to a body in which corruption has begun, rather than to a body which has recently been deprived of life. To my mind also not only are 'corpuscles' exhaled by them in large quantities but also they extend farther and strike more strongly the organs of those animals."

This recalls and substantiates what Sloane has written on the same subject (see page 95). But Labat further says:

"But a thing rather surprising, yet one which is however of public notoriety, is that these same fish more often attack an Englishman than a Frenchman, when they find them both together in the water. It may be that the Englishman has pores more open than the Frenchmen, and as a necessary consequence he will exhale more corpuscles proper to strike the organs of these fishes and hence attract them."

Labat next goes on to argue at some length that there is a difference in the "corpuscles" given off by members of two nations because of a difference in their foods and in their physical habit of body: that the Englishman, being a heavy eater of meats and of a hearty rugged habit of body ("beefy"), all in marked contrast with the more delicate-

bodied and daintier-feeding Frenchman, will "produce an exhalation of corpuscles whose odor is more penetrating, which scatter farther, and which strike more on the organs of these animals." This conclusion he backs up by quoting the cannibal Caribs that the flesh of an Englishman is more appetizing than that of a Frenchman. He also declares that the Carib trackers can follow an Englishman or a negro through the forests more easily than a Frenchman by simply smelling of their tracks, and by the odor can distinguish the nation of the track-maker. Then he argues that if this is so for men, why should it not hold also for the fishes.

Just what to make of this the present writer does not know. The whole matter depends on the strength of the sense of smell in fishes. This, in sharks at any rate, is quite acute. By pouring blood or by hanging overboard a carcass (the more decomposed the better) sharks may be readily enticed up current or up tide. This the present writer has done (1912). The odor from the negro is very offensive to the white man, and I have been told that to the Chinaman the odor of the white man is just as distasteful. As Labat says at the close of his discourse, each must be left free to make up his own mind as to the value of this conjecture.

Catesby's remarks (1754) on the danger to bathers of this fish are brief but to the point. "It is a swift-swimming and very voracious fish, preying on most others; and some of the largest size have frequently attacked and devoured men as they were washing in the sea." While Brown (1756), without specifically saying so, indicates his knowledge of similar habits on the part of the Jamaican fish.

Bullen (1904) quotes the apocryphal stories current throughout the West Indies as to the diabolical ferocity of the barracuda and ends by giving an eye-witness account of the fear of this fish which is universal throughout these islands. A pair of can-hooks had been lost overboard in 40 feet of water, and for a small reward a band of 8 negroes, swimming about the vessel and paying no attention to some sharks in the near vicinity, endeavored to recover these. All went well until the cry of "couter," "couter," was raised, whereupon bedlam broke loose. Crazed with fear, the negroes fairly climbed over each other to come aboard by the help of ropes flung out to them. Bullen adds that even when safe on the ship "their demoralized, panic-stricken condition was painful to witness." If the reader will, in this connection, examine Bullen's well-drawn figures of the barracuda (reproduced herein opposite page 55) and the other figures given in this paper of the head and jaws, and will recall the cold ferocity of this fish, he can better understand the truth of this story.

Holder (1908) had in his employ many years ago as guide and factotum on the outer Florida Reef a typical reefer who went by the common name "Barracuda." Because he was an expert at taking

this fish with the grains, Holder thought that he had been so named, but inquiries showed a totally different origin. It seems that years before this man had lived on Sea Horse Key in the Bahamas and had there got his name because of a horrible experience he had had with the barracuda fish. On the occasion of a great storm, a small ship was driven on the reef and all on board washed overboard and drowned save one woman who was lashed to the rigging. This man, McNally by name, threw off his clothes, tied a light line around his waist, and despite the dissuasions of his friends began his hard swim to the vessel. Several times on his journey he was seen to strike at something, and on his return (having sent the women in tied to the line), he was seen to fight with something and once was pulled under. His friends thought that he had encountered a shark, but when he came to shore it was found that both going and coming he had been attacked and seriously bitten by the fish whose name he afterward bore.

Further, Holder was told of a number of men who had gone overboard in channels between the Keys and who had been almost killed by these vicious fish. He also relates an incident, which seemingly fell under his own observation, of a barracuda which had been forgotten in the well of a fishing sloop. When a man went down into the well to repair it he was attacked by the fish and maimed for life.

Finally, as bearing out the present writer's statements at the beginning of this section, Henderson (1916) may be quoted that:

"As to the *picona* danger, not much can be said beyond mentioning the general fear of this aggressive fish. . . . He prefers rocky places about the reefs, where, lying motionless near the bottom, he darts at his prey with a swiftness that baffles the eye. His sinister appearance, astonishing quickness, and occasional habit of ranging the water in schools, like squadrons of submarine destroyers, have combined to give him a bad name. . . . As a matter of fact we feared these [barracudas] more than sharks."

Captain Wilson writes of the Bahama barracuda:

"I know of a case of a man who was walking quickly on a shallow reef beside deep water, and a barracuda flashed up and hit him on the foot. In this case, the cause, I think, was his white foot going in and out of the water quickly, for anything that moves quickly they will flash at. They give a ghastly bite."

Thus we have abundant evidence of the ferocity of *S. barracuda* in Gulf-Caribbean waters and of its dangers to man. Turning to the Pacific, it is interesting to note that the California form, *S. argentea*, which attains a length of 5 feet, is entirely harmless. In the southern part of this great ocean, however, is found the formidable *S. commersonii*, which has been known to reach the great size of 8 feet. On the authority of Andrew Garrett, Günther states that such large individuals are extremely dangerous to bathers. Much more circumstantial, however, is the following interesting present-day account

from Wood-Jones (1912). In this connection see his figure of such a giant fish reproduced herein as figure 2, plate 1. He writes:

"The barracouta has, however, left its mark upon at least one man, and I have seen a Cocos [Keeling Archipelago] native the whole of whose calf muscles had been torn away by the cruel teeth of this large [marine fish] relative of the pike. The barracouta is an ugly and dangerous fish, for it is of all sea creatures the most difficult to see, and it has a habit of dashing upon whatever stirs in the water."

In his very interesting book, describing the cruise of the *Curaçoa* among the South Sea Islands in 1865, Brenchley figures and describes the tie-beam of a house at Uji, Solomon Islands. On one side of this beam is carved and painted a scene showing an overturned canoe with the men fighting with sharks and other fishes which are devouring some of them. Concerning this scene Brenchley says: "Among the fish regaling themselves on the remains of the bodies which they have partially devoured are to be found more than one species. The long central fish is the Sphyræna, popularly known as the Barracuda." This tie-beam was brought away by the *Curaçoa* and figures of its two sides form the frontispiece of Brenchley's book. The figure of the barracuda, with a piece of human flesh in its jaws, is admirably drawn and perfectly recognizable.

Further west in the Indian Ocean the barracuda abounds in the waters around the island of Mauritius, where it bears the local name *tazarre*. Nicholas Pike, while United States consul at Port Louis nearly 50 years ago, made many valuable natural history observations. From his delightful book "Sub-tropical rambles" (1873) we learn that, whenever he went collecting in the tide-pools and over the shallow reefs, he always carried a fish spear to protect himself against attacks from barracudas and eels. He tells us that once he was attacked by a *tazarre* of considerable size, which "came right at me like a bulldog." He harpooned it in the side, but it got away and then came at him the second time. This time he struck it in the head, but held it off with difficulty, though he was a large powerful man.

## HABITAT.

The barracudas comprise the sole genus of the family Sphyrænidæ. There are some 20 species of these carnivorous salt-water "pikes" found in the warm seas (tropical and sub-tropical) all over the world. Jordan and Evermann (1896) list 7 species from North American waters: 2 from the Pacific Coast; 4 from the Atlantic; and 1, a European form, from the Bermudas only (on the authority of Dr. Goode). Of the Atlantic forms 3 seem to be wholly tropical, ranging from Pensacola and Charleston to Bahia; 2 of these are occasionally taken as far north as Wood's Hole, probably as stragglers in the Gulf Stream; the other (the northern barracuda), seems to range from Cape Cod south to

about Cape Fear. The young are not infrequently taken in Beaufort Harbor, though the adult is unknown there. So far as its habitat is concerned, the northern barracuda seems to be a decidedly aberrant form.

Equally aberrant is the form found on the west coast of Africa. Reeve reports (1912) that it goes up the Gambia River, 160 miles, to McCarthy Island, where the water is perfectly fresh. He notes that such specimens are very thin, and conjectures that they find it difficult to get sufficient food. Whether this barracuda is the *Sphyræna jello* reported by Büttikofer for the Liberian coast, as elsewhere noted, can not be said.

## FOSSIL FORMS.

Our knowledge of the Sphyrænidæ far antedates the historic period; even Aristotle's mention of them is comparatively recent. In the Cretaceous seas which covered Kansas and the adjacent parts of the Great Plains region, and in the bays and shallow sounds along the North Carolina coast, there disported themselves in large numbers certain fishes of powerful frame and voracious habits to which the paleontologists have given the name *Protosphyrænidæ*, the first sphyrænas. The generic name was assigned to these fishes by Leidy as early as 1857, but it seems that Agassiz much earlier than this had examined the teeth of the same form and had erroneously placed their owners among the Saurocephali. There is, it must be confessed, some doubt about the affinities of these fishes. Indeed, Jordan (1905) says "the jaws are armed with very strong teeth, as in the barracuda, which however the species do not resemble in other respects."

Two of these Protosphyræna fish are known by the specific names of *Protosphyræna nitida* and *perniciosa*. Careful perusal of the literature would probably give the names of a number of other species referable to this fossil genus. However, it is not the purpose of the present writer to go into the matter of fossil forms further than to call to the attention of the reader the fact that the fossil Protosphyrænids are by many considered as the ancestors of the modern Sphyrænids. So Felix (1890) seemed to think, and his figure of *Protosphyræna nitida*, reproduced herein as figure 25, plate VII, certainly does show the head of a fish whose teeth and jaws are remarkably like those of the big barracuda. Attention is called to the two great canines in front and to the knife-shaped teeth of the upper and lower jaws. The teeth of the upper jaw are seen outside those of the lower, but whether this is natural or an artifact can not be said—possibly both, and rather certainly the latter, since the great canines are also found outside the lower jaw-bone. However, from the drawing they seem to be rooted in the premaxillary.

Louis Agassiz (1843) also figures in the atlas to volume V of his great work on fossil fishes two skeletons of certain fishes which he does

not hesitate to call *Sphyræna*. These skeletons are from the Eocene of Monte Bolce in Italy. The first is called *S. bolcensis*, from its place of discovery, and is based on a number of skeletons from different museums. The second is *S. gracilis* and several specimens are known. These are reproduced herein as figures 23 and 24, plate VII. Attention is called to the shape of the snout and to the upper teeth in figure 24, and to the 24 vertebræ (the proper number) in figure 23.

In 1901, the distinguished paleontologist Dr. A. S. Woodward catalogued the Sphyrænid material in the British Museum and reduced most of the previously described forms to synonymy. He sets up three distinct species: *Sphyræna bolcensis*, *intermedia*, and *suessi*. Six other species are quoted from earlier writers, but Woodward thinks the material from which they were described to be so imperfect (in one case consisting of a single tooth only) as not to justify the erection of species upon it. All the valid material is from the Eocene of Monte Bolce near Verona in northern Italy. Woodward throws out Agassiz's *S. amici* from Mount Lebanon as not belonging to this genus.

## NOMENCLATURE.

The generic term *Sphyræna* means hammer, according to Jordan and Evermann (1896), and hence the barracuda is a hammer-fish—a total misnomer since it resembles nothing so little as a hammer, as was noted so long ago as 1554 by Salviani. This erroneous derivation and interpretation seem to have come about somewhat as follows: The name *Sphyræna* originated with Aristotle, who, in his "Natural History," book IX, chapter 3, 610*b*, 5, simply names the fish. However, it will be shown further on that the more common name among the Greeks was *cestra* (a kind of light javelin invented and used during the Persian war) and also a goad or pointed stick. The word *Sphyræna* apparently has its origin in the word *sphyra*, a hammer, but *sphyræna* has no use or meaning other than as the name of the fish under consideration. This statement is based on the authority of Professors Gildersleeve and Miller of the Johns Hopkins University. The name *cestra*, however, seems to be a definite allusion to the shape of the fish and its pointed head.

Our next authority is Pliny. In his "Natural History," book XXXII, chapter 11, paragraph 54, he speaks of the fish "called *sudis* in Latin, and in Greek *sphyræna*, names which indicate the shape of its snout." This *sudis* or *sudes* was a kind of javelin and also a kind of stake somewhat pointed and hardened in the fire. Furthermore the colloquial name used along the Mediterranean shores of Italy, France, and Spain to-day is spet or spetto. This term has already been used in this paper in speaking of the European fish, and refers to the elongated form and pointed snout.

The etymology of this name is very obscure. *Sphyræna* = hammerfish is such a misnomer that I set to work to puzzle it out. Rondelet (1558) makes *sphyræna* = *cestra*, a sharpened stake, because of its pointed snout. Cuvier and Valenciennes (1829) cast strong doubt on the hammer-fish derivation and definitely state their belief that *cestra* (javelin or stake) is a synonym for *sphyræna*, in allusion to its pointed snout. This led me back to Conrad Gesner's "Historia Animalium," IIII, where was found a wealth of material which is summarized below. In this connection I wish to express my thanks to Professor C. W. E. Miller, of the Johns Hopkins University, to whom I am indebted for translations of and some keenly critical comments upon the names used. These translations and comments have gone far towards clearing up the situation and for confirming the authors referred to in this paragraph.

Before dealing with the data found in Gesner, it may be well to state that Aldrovandi (1613) is in full accord with Gesner, whom he quotes in large degree.

Gesner (1558) quotes the Greek poet and philosopher, Epicharmus, who flourished at Syracuse about 485 B. C., where he speaks of "*cestras* and shining perches." Next he notes that Speusippus (about 407 B. C. to 339 B. C.), the nephew and disciple of Plato, likened the *sphyræna* or *cestra* to the fish called in Latin *acus* (gar-pike). Then he finds that Athenæus, the Greek philosopher of Naucrates and Alexandria, Egypt, in his great work, "Deipnosophistæ" (about 200 A. D.), writes that "Dorian says that what they call the *cestra* is the *sphyræna*, and when Epicharmus called it the *cestra* he no longer said *sphyræna*, although they are the same. And the Attic Greeks more often call the *sphyræna* the *cestra* and very seldom use the name *sphyræna*." These quotations make it clear that the two names were used interchangeably but that *cestra* gradually came to be used almost exclusively for the fish once called *sphyræna*.

Thus *sphyræna*, *cestra* (or *kestra*), and *sudis* were all used synonymously for a certain slender sharp-headed fish recalling the idea of a javelin, a pointed stake, or the prow of a ship. Now there enters on the scene one Theodorus Gaza, a learned Greek scholar who was born about 1400 and who died about 79 years later. The Turks having captured his birth-place, Thessalonica in Macedonia, he was driven into Italy, where he was for many years professor of Greek at Ferrara. Later he moved to Rome and engaged in translating Greek works into Latin, among them Aristotle's "Natural history of animals" (1476). Gaza translated *sphyræna* = *kestra* = *sudis* by the Latin word *malleolus*, hammer, and hammerfish it has remained to this day.

Now *the* hammerfish is *Sphyrna zygæna*, the hammerhead shark, and on this point Gesner definitely says that the common codices or texts of his day were full of errors, *zygæna* being often written for *sphyræna*

and *vice versa*. The hammerhead shark gets its name (*sphyrna*, hammer; *zygæna*, yoke) because the laterally elongated lobes of its head stand out from the body, giving the head end of the fish the shape of the Greek letter $\tau$. Further, Gesner says that at Marseilles there was a hammer-fish called Jew-fish, which by many was thought to be a *sphyræna* but which was really a *zygæna*. Then he quotes the French ichthyologist Gilles, that the hammer-fish of Marseilles was a *zygæna*, and that it was called a Jew-fish because its lateral head projections much resembled a kind of head-dress having lateral horns formerly worn by certain Jews of that city. Furthermore, it is interesting to note that the specific name given to the hammerhead shark by many ichthyologists is or was *malleus* (hammer). From all this we may easily see how the names were confused.

However, this etymological tangle is not so easily unraveled as the preceding paragraph seems to show. *Sphyræna* probably has its origin in the word *sphyra*, which means hammer. Gaza gives as a synonym the Latin word *malleolus*, and this has added further to the complexity. The word *malleolus* means a little hammer, and Professor Miller writes me that it is neo-Latin for the tibia and fibula with their enlarged ends. These in Greek are represented by the word *sphyron*, which also means hammer. And so it seems that we have come to a *cul de sac*. Now let us return to *cestra* and see what we can get from it.

Pollex (born at Naucrates, Egypt, about 130 A. D.) has left us a dictionary of Greek words in which "*cestra*" is defined as "a certain kind of hammer"; but what kind? Professor Gildersleeve writes that it was "an agricultural implement employed in breaking up clods." And Professor Miller says that it was a double-headed hammer, flat on one head and with the other pointed, a pick hammer or "*Spitzhammer*," such as geologists use. Such hammers are figured among the illustrations in archeological works. Now the error of preceding writers is clear. Deriving *sphyræna* from *sphyra*, hammer, and either overlooking *cestra* in its meaning of javelin, or using *cestra* as hammer without going into critical study of what kind of hammer, they have in all cases made *Sphyræna* the hammerfish, when it should be the *pickhammer* fish, the name being given not in allusion to the hammer end of the tool but to the pick end. Hence *Sphyræna* is not the hammerfish but the *pickhammer* fish, and it is seen that the name plainly alludes to the shape of the head and snout, and that it is a synonym for *cestra* and for *sudis*.

On the origin of the specific name, barracuda, I regret that I am unable to throw any light. Walbaum in 1792 seems to have first used it for the name of the species. So struck was he with the similarity of this fish to the fresh-water pike, that he named it *Esox barracuda*. He, however, simply gave his so-called "pike" the native name barracuda with which Catesby had labeled his drawing from a Bahama specimen in 1731.

The use of the name, however, antedates Catesby. Sloane (II, 1725) uses it. Dampier, whose sixth edition (published 1729) I have, refers to this fish under the name "Parricoota." Dampier's second visit to Campeachy, where he first saw or at any rate described the "Parricoota," was made in 1676. In book II, chapter 2 (p. 144), in which the fish is referred to, Dampier says that "About the middle of February 75–6, we sailed from Jamaica" for Campeachy and after a short and safe voyage arrived there. Dampier's Voyages are written directly from his manuscript journal, and the accounts on pages 171–2 of his printed book are dated 1676, so at least to this date the name *Parricoota*, a corruption of the apparently native word *barracuda*, can be traced. Probably a close search of the early Spanish chroniclers and writers on the natural history of the West Indies would show the name in use long before Dampier's time.

This name, in its various spellings (barracuda, barracouta, barracuta, parricoota, paracuta, etc.), has become wide-spread, being the common name for the fish wherever found the world around.

The other colloquial name, picuda, seems to have been given the fish by Parra in 1787. This is a Spanish term, having its root in common with our English word pike, given in plain allusion to the similarity in form and habits between this fish and the fresh-water pike.

The name becune is French in origin, and it will be recalled as the name used by Rochefort, De Tertre, Labat, and Fermin. This is the Gallicized form of the medieval Latin word *becuna* according to the Century and Standard Dictionaries. However, not being content with this, I asked Professor Miller to pass on these names also, and he kindly writes that *bécune* is French and is borrowed from the Spanish *bécuna*. He notes that the first syllable of these words corresponds to the French word *bec*, beak of a bird or snout of a fish, and that the Latin word *beccus* is of Gallic origin. The *-une* or *-una* is simply a termination. Hence *becune* or *becuna* means *beak-fish*.

In this connection, Professor Miller makes the interesting suggestion that, since *sphyra* conveys no suggestion of sharpness or pointedness, as does the word *cestra*, possibly the name may have been given in allusion to the hammer-like swiftness and force of the fish's attack. Then he adds: "The *sphyræna* would then be hammer-fish; the *cestra*, the pickhammer-fish; the *sudis*, the stake fish; the *becuna* (*becune*), the beak-fish: according to the varying point of view of the observer."

## DRAWINGS OR FIGURES OF THE BARRACUDA.

The history of the big barracuda has been rather fully given in the course of this paper, and little can be added here. However, it may not be without interest to give some few points about figures of the sphyræna, both European and American.

Belon seems to have published the first known figure of the European sphyræna, but Cuvier and Valenciennes say that it was incorrectly

drawn. I have not seen this, nor have I had opportunity to examine Rondelet's original figure published in the Latin edition of his book in 1554. His figure in the French translation of the above work is the earliest examined in the course of this research, but there is no reason to doubt that it is not identical with that in the 1554 folio. The figure is small and not very distinctive. Cuvier and Valenciennes say that the head is too long. This figure was copied by Gesner in the fourth volume of his "Historia Animalium" (1558). Aldrovandi (1613), however, had a new drawing made for his book, but our French critics say that it was made from a dried specimen. While in some ways an improvement on the preceding figures, it is not a good drawing, the head especially being poor. These writers also say that Bloch's figure —which I have not examined—is the best made up to that time, but that it is faulty in some respects.

However, of the figures studied, Salviani's (1554) is far and away the best portrayal of the sphyræna, either European or American, made prior to the time of publication of Cuvier and Valenciennes' elegant drawing to be referred to later. Occupying a whole page in Salviani's folio, it is well drawn and well printed. There are some defects. The teeth are not figured absolutely correctly and the ventral and caudal fins are not well done, but the figure as a whole is distinctly good. The eye is fine, the head generally well done, the lower jaw is longer and has a distinct lump at the upturned end. The point of the upper jaw is plainly upturned and slightly hollowed out for the reception of the great tooth at the point of the lower jaw. The fins are well placed, as is also the lateral line. Most noticeable is the absence of the first dorsal fin and this absence is severely criticized by Cuvier and Valenciennes. However, Salviani distinctly says that there are two dorsal fins, "the first on its middle, the hinder one, however, towards the caudal." In the dead fish, this is always sunk in the sheath, and so it was in the specimen from which Salviani's artist made his drawing. It is greatly to be regretted that this striking figure was not studied until the present paper was in press. Had it been seen earlier it would have been reproduced herein.

The earliest figure of the American fish which has come to light in the course of this research is Rochefort's drawing of the *becune* taken from the edition of his book published in 1665. It is a poor figure, giving only in very general outline the form of the fish and the relative position of the fins. The most striking defect consists in the absence of one set of the paired fins, just which it is hard to say. However, historically it is of enough interest to be reproduced herein as figure 15, plate v. There is reason to think that this figure appeared in the first edition of Rochefort's work in 1558, which I have not been able to consult.

The next ancient figure is that in volume II of Sloane's "Voyage to Jamaica" (1725), table 247, figure 3. This, however, is so poorly

drawn as to have nothing about it to distinguish it as a barracuda save the name appended below. For these reasons it is best to omit any reproduction of it here. Almost as bad is Labat's (1742) reproduction of Rochefort's figure (1667), since Labat leaves off the lateral line, possibly because Rochefort had drawn it incorrectly.

Next in point of time comes Catesby's drawing of the Bahama form. While this is crudely done it seems worth while from the historical standpoint to reproduce it in this paper as figure 16, plate v.

The next figure of the big West Indian barracuda is Parra's drawing, reproduced herein as figure 17, plate v. It was published in 1787 and, though crude, is by far the best of all the figures published prior to 1829.

The first really accurate delineation of *Sphyræna barracuda* is that found in the third volume of Cuvier and Valenciennes. This is really a wonderful drawing to have been made from a preserved specimen. The reader will find it given herein as figure 18, plate v. The one criticism is that the head is somewhat too short and blunt.

After Cuvier and Valenciennes' elegant figure, the next portrayal known to me is that found in volume IV of Jordan and Evermann's great work on American fishes. This excellent figure has but two defects worthy of serious criticism; the lateral line runs straight where it should rise over the pectoral fin; and the fin rays do not correspond to the count in the text. This drawing is herein reproduced as text-figure 2. These same authors, in their "American food and game fishes" (1905), publish an excellent figure, apparently a photograph of a preserved, possibly a still fresh specimen, viewed from the side and slightly from below. This fine figure shows the lateral line markedly arched over the pectoral fin, but the authors persist in their statement that it is straight.

Very valuable are the three portrayals in the plate taken from Bullen's book (1904) and reproduced herein facing page 55. These are by long odds the best figures extant of this fish, and portray very closely attitudes in which the fish has often been observed at Tortugas.

The observations on the living fish, its structures and habits, and the collection of material and data for further study were made at the Tortugas Laboratory of the Carnegie Institution of Washington. Here Dr. A. G. Mayer, the director, did everything possible to forward my work. The historical side of the paper was worked up in the Library of Congress and the Library of the United States National Museum. To the officials in charge of these two great libraries I am under obligation for many courtesies. The extracts from the various authors referred to are in the main literal quotations. Transliterations would possibly have enhanced the appearance of the paper, but experience has taught me that verbatim quotations are far more valuable to the reader.

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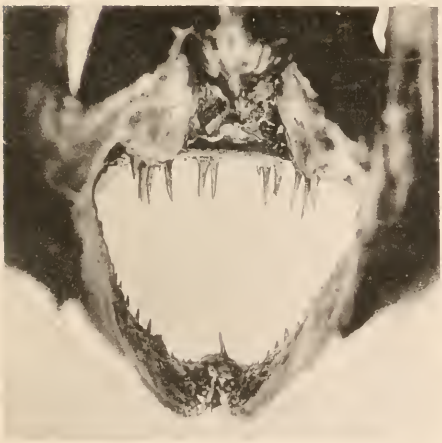

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3. Head of *S. barracuda* seen from above, fresh specimen.
4. Lateral view of same head.
5. Looking into mouth of barracuda from behind, Miami specimen.
6. Under side of dried head showing apertures behind point of lower jaw, and also socket in apex of upper jaw for reception of solitary mandibular fang.

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7. Mouth and jaws of 55-inch barracuda, dried head.
8. Mouth and jaws of fish figured in Plate I, dried head.
9. Mouth of *S. barracuda* showing teeth, tongue, mandibular breathing valve and spaces to receive palatine teeth — dried head of fish figured in Plate I.
10. Mouth showing teeth and mandibular breathing valve with depressions to receive great fangs of upper jaw. From same head shown in figure 7, this plate.

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11. Dorsal view of skull with upper jaw displaced forward showing joint between the two.
12. Ventral view of the same.
13. Lower jaw showing teeth and also sockets in mandibular bones for reception of premaxillary fangs.
14. Ovary of 55-inch barracuda.

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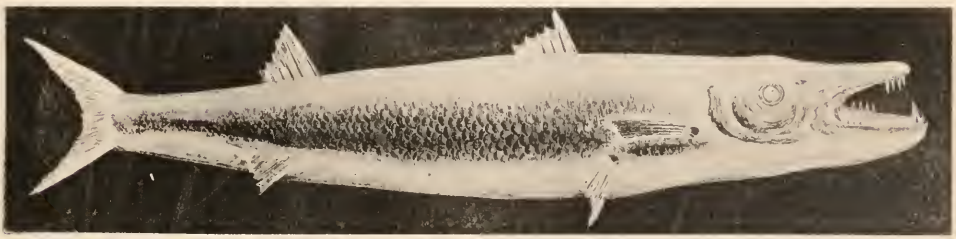

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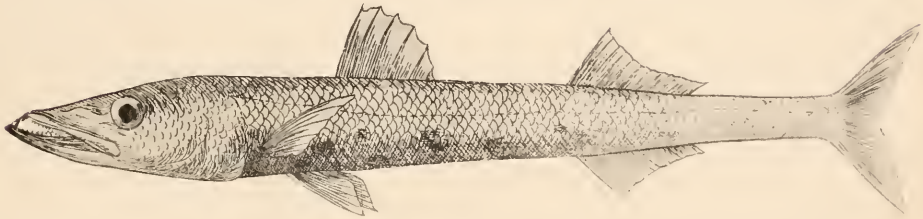

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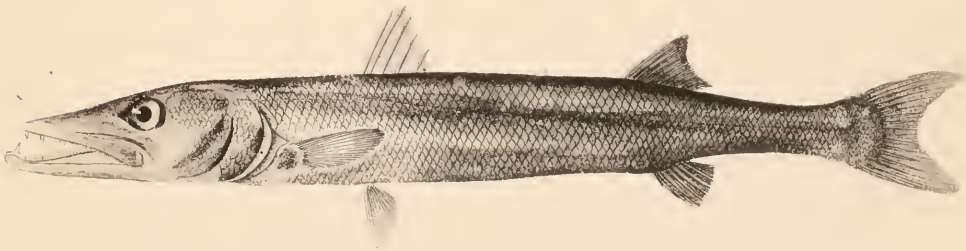

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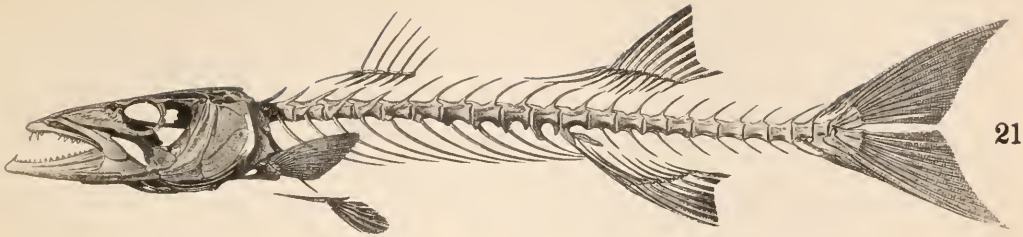
15. Becune, after Rochefort, 1665.
16. Barracuda, after Catesby, 1754.
17. Picuda, after Parra, 1787.
18. Sphyrène, after Cuvier and Valenciennes, 1829.



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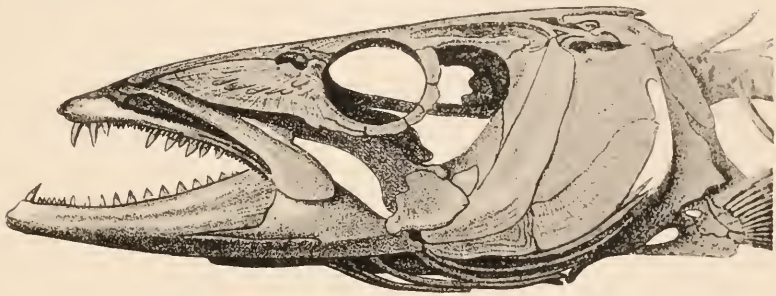

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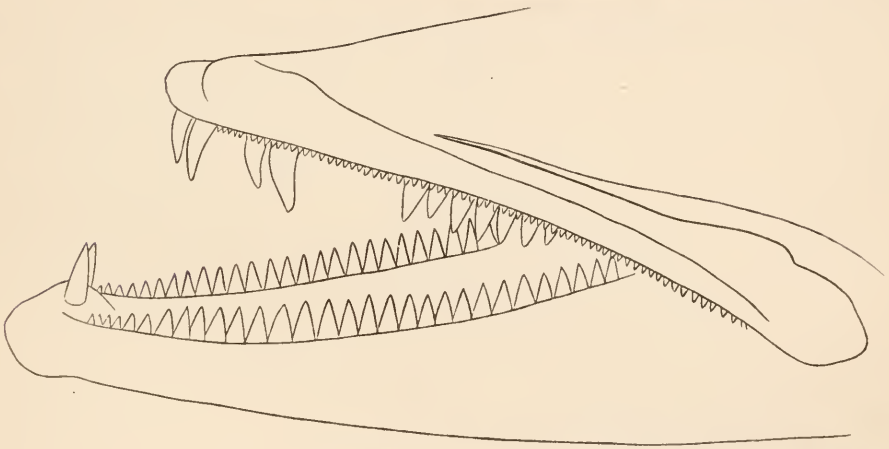

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19. Much enlarged line drawing of head from Cuvier and Valenciennes.
20. Enlarged head from Cuvier and Valenciennes, colored figure, plate V, figure 18.
21. Skeleton of *S. barracuda* after Agassiz, 1843.
22. Head of the same much enlarged.

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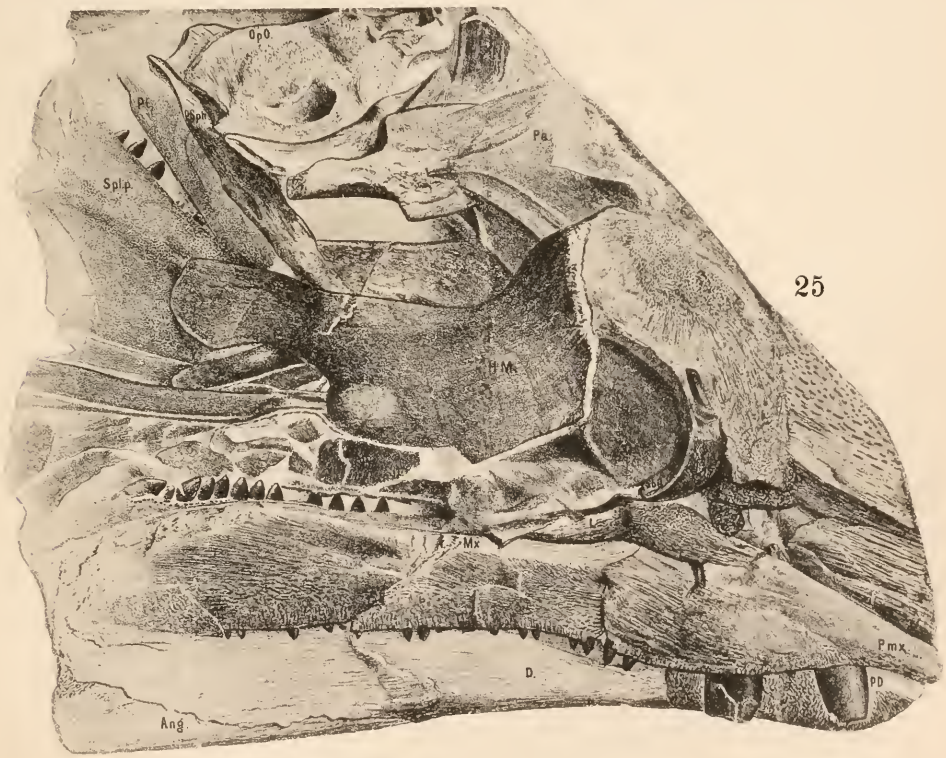


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23. *Sphyræna gracilis*, after Agassiz.
24. *Sphyræna bolcensis*, after Agassiz.
25. *Protosphyræna nitida*, after Felix.

V.

# BOTANICAL ECOLOGY OF THE DRY TORTUGAS.

By H. H. M. BOWMAN
Of the University of Pennsylvania

Six plates and seven text-figures.

# BOTANICAL ECOLOGY OF THE DRY TORTUGAS.

By H. H. M. Bowman.

As the name of these islands indicates, their vegetation is characteristically xerophytic, although the rainfall is sufficient to assure the plants the necessary amount of water. Living in such a difficult environment, as may be supposed, the plants are very interesting when a close study is made of their individual characteristics. The opportunity for such study was given the writer during the summers of 1915 and 1916, while pursuing another line of botanical research under the auspices of the Carnegie Institution of Washington, which partially controls one of them (Loggerhead Key), where a marine laboratory is maintained.

The Dry Tortugas are situated in the Gulf of Mexico between 24° 34′ and 24° 42′ north latitude and between 82° 48′ and 82° 58′ west longitude. The relative distances in the cardinal directions of points on land are as follows: approximately 920 miles east of Tampico, Mexico; 625 miles southeast of New Orleans; 470 miles south by east of Pensacola; 70 miles west of Key West, and 90 miles north by west of Havana. The Tortugas are really the westernmost of all the Florida Keys, but are more detached from them and have different geological and botanical aspects.

## GEOLOGIC FORMATION.

The geological formation and the history of south Florida and the adjacent regions have been investigated thoroughly by T. Wayland Vaughan, of the United States Geological Survey, and in one paper he discusses particularly the Tortugas Atoll.[1] From this paper the writer quotes largely as to the geology of these islands. The Dry Tortugas consist of eight small islands: Loggerhead Key, Bird Key, Garden Key, Long Key, Bush Key, Sand Key, Middle Key, and East Key; these, together with large submerged banks and several shoals which were, until recent hurricanes, charted as islands, form an irregular ellipse with its longer axis directed from northeast to southwest. The lagoon inside of this atoll has a depth of 5 to 7 fathoms.

As stated in Vaughan's interesting account, two lines of investigation were taken up in determining the geology and origin of the Tortugas atoll: first, whether submarine solubility phenomena played an important part in their history; second, whether the wind and current

[1]Vaughan, T. Wayland, The Building of the Marquesas and Tortugas Atolls and a Sketch of the Geologic History of the Florida Reef Tract. Carnegie Inst. Wash. Pub. No. 182, pp. 55–67.

action were responsible. To determine the first, a chemical research was conducted into the dissolving power of sea-water due to the $CO_2$ it contained, and the material from the bottom of the lagoon was examined. This latter examination showed the bottom to be fine calcareous mud, precipitated by denitrifying bacteria, as discovered by Drew.[1] The former chemical research was made by Dole[2] on daily observations of the amount of $CO_2$ in the sea-water flowing into the lagoon and the amount of carbonates in the water flowing out. The result of this work showed that the dissolving action of $CO_2$ in the water was negligible and from the bottom samples it was ascertained that deposition was going on at a rate far exceeding any solubility.

The above study eliminated the first theory of action by solubility, but the theory of formation by waves and currents remained. As observed by various writers, sand dunes and water-carried detritus are alike molded into two shapes by certain wind and water currents. The latter are formed by an obstacle or a counter-current shearing a constant current, which drifts material to both sides and a crescent is formed with the bow of the arc facing the current. Vaughan further says that there are three kinds of currents working in this region: first, wind-formed currents, accompanied by waves; second, the Florida counter-current; third, tidal currents. The prevailing wind in the Tortugas is from northeast to southwest, and the islands also lie in the sweep of the Florida counter-current, which moves west, so that these two sorts of currents cooperate; on the other hand, the general tidal current is from north to south—*i. e.*, flowing transversely to the two before mentioned; thus the arc of the Tortugas Atoll is bowed toward the east, against the prevailing wind and the counter-current. The southwest part of the perimeter trails along the direction of these currents. The southwest and southeast passages in the atoll are attributed to the influence of the counter tidal current. White Shoal and Brilliant Shoal indicate the direction of this current, while Loggerhead, the largest of the group, shows the elongated "linear-ridge" shape due to the deposition of material by currents trailing along from the tails of the crescent, and the indurated beach rock on this island shows it to be wave-built, by its seaward slope.

On Garden Key, as seen by borings made by Vaughan, the larger rock-masses were found to be massive dead coral-heads. All of the Tortugas Keys are composed of calcareous detritus, the remains of various $CaCO_3$-secreting organisms, mollusks, corals, nullipores, echinoderms, and the calcareous algæ. The coral fauna of the Tor-

[1]Drew, G. H., On Precipitation of $CaCO_3$ in the Sea by Marine Bacteria and an Account of Denitrifying Bacteria in Tropical and Temperate Seas. Carnegie Inst. Wash. Pub. No. 182, pp. 7–45.

[2]Dole, R. B., Some Chemical Characteristics of Sea-Water at Tortugas, Florida. Carnegie Inst. Wash. Pub. No. 182, pp. 69–78.

tugas, which has also been extensively studied by Vaughan, is quite rich and has contributed a great deal to this detritus. The atoll is therefore formed by certain currents arranging this loose calcareous detritus. This material above sea-level is unconsolidated, but below 8 feet indurated beach-rock is found. This constituted an older formation for the growth of reef corals. "It is probable," Vaughan says, "that this rock was sub-aerially indurated and then depressed—*i. e.*, the atoll was outlined previous to coral growth in this region." The whole of the south Florida region was deposited in Pliocene times during depression; then in Pleistocene time there was an uplift and again a depression with a succeeding uplift. During the Pleistocene period it is supposed that some of the coral reefs stood as much as 18 feet above sea-level. In recent times there has been a depression, which, however, has left the keys slightly higher than they were before the Pleistocene depression. The evidence of these oscillations is borne out by the knowledge of the growth habit, in relation to sea-level, of the reef-forming corals in the Florida region.

## CLIMATIC CONDITIONS OF THE TORTUGAS.

While no permanent records are available from the Tortugas, the writer assumes that the records from the office of the United States Weather Bureau at Key West, only 68 miles distant, will for this purpose be applicable to the climate of the Tortugas. The records in this office have been kept since 1871 and are very reliable.

For botanical consideration the subject of rainfall is quite important. According to the Key West records the total average rainfall is 38.66 inches. The precipitation is quite varied and depends largely in summer on tropical squalls which suddenly appear on the horizon and sweep over the islands with a fierce rush of wind and driving torrents of rain. These perhaps last only 20 minutes to an hour. The maximum total precipitation for 24 hours, for the year 1914, for instance, was 4.80 inches, which occurred in November of that year. An idea of the variation may be gained by comparing this with the maximum precipitation for 24 hours in January of the same year, which was only 0.31 inch. It may be mentioned in this connection that the greatest precipitation in this region occurs during the months of September, October, and November. As stated above, the average annual rainfall for Key West (and presumably the approximate for Tortugas) is 38.66 inches. By comparing this with the total average precipitation for Miami, situated on the mainland of Florida, 125 miles north of Key West, which is 46.56 inches, it is seen that the average is slightly lower for the southern keys than for the main peninsula.

The average number of clear days for these southern keys is 151. During the summer months of May, June, and July the writer has

lived in the Tortugas, when for periods of several weeks there was a continuous succession of clear, brilliantly sunny days with not even an occasional tropical storm or squall. According to the meteorological summary for Miami, the total average of clear days is only 68 and partly cloudy 135. The comparison again, with the record for Key West, with its average of 151 days, taken together with the difference in total precipitation, shows the climate of the southernmost keys to be slightly drier than that of the mainland. This difference is perhaps due largely to the prevailing winds.

The prevailing winds are eastwardly, as reported by the Weather Bureau at Key West, and as also observed at Tortugas by Vaughan, in his paper on the influence of the prevailing wind in atoll formation, and also by the writer in various physiological experiments undertaken at the latter place. The velocity of these winds is very variable. The average velocity is 9.6 miles per hour. But in this region of hurricanes all winds over 75 miles per hour are rated as hurricane winds. These usually occur in the fall during the months in which the heaviest precipitation occurs, viz, September, October, and November, which months are called the "hurricane months." In the Gulf region, as recorded by the Key West office, the following severe hurricanes, of which the directions and velocities are here given, did a great deal of damage: On September 25, 1894, 87 miles per hour from the southwest; October 19, 1896, 88 miles per hour from the southwest; October 11, 1909, 83 miles from the northeast; October 17, 1910, 100 miles per hour from the south. This last hurricane, known as the "great hurricane of 1910," not only did vast damage on land but, as observed by the writer and others by means of a diving helmet and glass-bottomed boats, the coral and sponge fauna and the algal flora of the sea-bottom in the region suffered great changes and in some places on the bottom immense windrows of broken corals may still be seen which were mashed and heaped up by the force of giant wind-driven waves.

The temperature of the Tortugas is fairly constant. The variations in January and February, which are the coolest months, range from 60° F. as a minimum for these months to 75° F. as the maximum; in June, July, and August, which are perhaps the hottest months, the minimum is 77° F. and the maximum 88° F. The Key West records show the average annual temperature to be 76.8° F. and for the entire period over which the records extend—*i. e.*, 1871 to 1913 inclusive—the maximum was 100° F. and the minimum 41° F. For Miami the mean annual maximum temperature is 80° F. and the minimum is 68° F.; that is, the annual mean temperature is slightly lower than that of the Tortugas and the southern keys.

## GENERAL SKETCH OF THE VEGETATION OF THE TORTUGAS.

On ecologic and geologic grounds the Florida Keys have been divided into four groups by Small:[1]

(1) The upper sand keys, which are really detached portions of the coastal peninsula and support a sand-dune and hammock flora closely related to the mainland.

(2) The Upper Keys, extending from Soldier Key to Spanish Harbor, and which are composed of a coral rock. These have a vegetation of tropical hardwood trees and shrubs and palms resembling those of the Bahamas which lie slightly to the east of them.

(3) The Lower Keys from No Name Key to Key West. These have a basic formation of Miami limestone. The flora of the group, according to Small, who has done much systematic work in this region, is quite varied, having large areas of pineland and palms as well as extensive hammocks. This flora is more closely related to Cuba, which lies only 90 miles to the south of this group.

(4) The group most directly considered in this paper is called the Lower Sand Keys. They are all the keys lying west of Key West and are composed of sand or, more strictly, according to the above analysis of Vaughan,[2] of coarse calcareous detritus, the remains of various organisms. Of these Lower Sand Keys Small[1] says "they are little more than sand bars and they support, like the ocean side of all the Florida Keys, only or mainly the characteristic strand flora of most of the West Indies."

The origin and relationship of the Tortugas flora may thus easily be traced to the adjacent large islands of the Antilles, Cuba, etc. The majority of the plants in the Tortugas are easily transported by the sea, as indeed are most strand floras.

A typical ecological formation in the Florida Key region is the mangrove association, *Rhizophora mangle*, but this association is entirely lacking in the Tortugas, owing to the physical nature of the islands. In the writer's work with *Rhizophora*, he observed that the floating hypocotyls must have a secure anchorage, either in the deep, soft mud amid the entangled roots of a mangrove swamp, or in the clefts and cracks of a coral rock, a mud-flat, or oolite bottom. The same plummet-like action of a young mangrove hypocotyl in boring a resting-place for itself in soft mud, or in finding a cleft by its twirling action in the water-currents, was observed by Crossland[3] on the Zanzibar reefs. The sand beaches of the Tortugas do not furnish the required conditions for the young viviparous seedling. The lack of sufficient

[1]Small, J. K., Flora of the Florida Keys. 1913, III–IV.

[2]Vaughan, T. Wayland, The Building of the Marquesas and Tortugas Atolls and a Sketch of the Geologic History of the Florida Reef Tract. Carnegie Inst. Wash. Pub. No. 182, pp. 55–67.

[3]Crossland, C., Note on Dispersal of Mangrove Seedlings, Annals of Botany, XVII, p. 267

moisture in the coarse, porous sand, together with the dry winds, soon kills the drifted young mangrove. This has been demonstrated many times in the physiological experiments of the writer on *Rhizophora* and explains the absence of the mangrove association in the Tortugas.

The plants of the Tortugas, living as they do in such uniformly xerophytic conditions and on such small areas of land, are naturally confined to a small group called a strand flora, on account of characteristic species which occur on all maritime shores and particularly tropical coasts—such genera as *Scævola*, and even the species *Ipomœa pes-caprœ* as found on all tropical beaches, as far as the remote islands of the Pacific, according to Guppy[1] and Schimper;[2] the latter, in his Plant Geography,[3] in his classification of tropical littoral formations calls the open sandy formation a "pes-capræ formation"; Harshberger[4] also includes a great many species found scattered all over the Tortugas in his treatment of sea-strand formations in South Florida, from which, however, the Florida Keys are excluded.

Broadly, it may be said that the entire flora of the Tortugas is a strand flora, but to the close observer these plants are easily seen to fall into certain associations or groups of several species. The reason for this grouping of species in a fairly uniform flora the writer believes to be due to two factors: first, the prevailing winds, which frequently carry dense salt spray or mist inshore, and certain of these strand plants are better able to withstand this drenching with a rather strong solution of sodium chloride and magnesium and calcium carbonates, of which latter salts the sea-water contains, in this region, fairly high percentages;[5] second, the aggressiveness of certain species and the ability to hold a position occupied by them against invading species—for instance, few plants will advantageously invade an area occupied by *Opuntia*, even though the surface is not entirely covered by its sprawling joints.

The writer, then, recognizes four fairly marked associations in the general Tortugas flora of strand plants: (1) the *Uniola* community; (2) the *Suriana* community; (3) the *Opuntia* community; (4) the *Chamæsyce* community.

The first association, the *Uniola* community, is rather heterogeneous and varies slightly on different beaches, depending on the conditions in rough weather and the prevailing winds. The lowest on the beach and close to the high-tide limit is *Cakile lanceolata* (Wildenow) O. E. Schulz. The dried stalks of this may be seen in July, and during August they

[1]Guppy, H. B., Observations of a Naturalist in the Pacific. 1913.
[2]Schimper, A. F. W., Die Indo-Malayische Strandflora.
[3]Schimper, A. F. W., Plant Geography upon a Physiological Basis. 1903, p. 387.
[4]Harshberger, J. W., The Vegetation of South Florida. Wagner Institute of Science, Philadelphia, 1914, vol. VII, pt. 3.
[5]Mayer, A. G., Annual Report of Director of Department of Marine Biology, Carnegie Inst. Wash., 1910, Year Book No. 9, p. 122, quoting from Report on Analysis of Tortugas Sea-Water, by Division of Physical and Chemical Research, U. S. Geol. Survey.

are uprooted and blow about the beaches as tumble-weeds. Growing with *Cakile* is the sand-spur, *Cenchrus incertus* M. A. Curtis, which forms large flat mats on the beaches, bearing its spikelets in a heavy spiny involucre, making a painful wound if stepped upon. Associated with this in dense masses the sea purslane (*Sesuvium portulacastrum* L.) is often seen; resembling it superficially is *Alternanthera maritima* St. Hildmann. Back from the reach of spray is *Sporobolus virginicus* (L.) Kunth; frequently out in line with it is *Tournefortia gnaphalodes* (Jacquin) R. Brown, forming large characteristic, flat-topped bushes 1 to 1.5 meters tall, clothed with soft, whitish-gray, tomentose leaves. The long, trailing vines of the purple beach morning-glory, *Ipomœa pes-caprœ* (L.) Sweet, are found here, and also *Scœvola plumieri* Vahl, in clumps with thick, glossy leaves, nauseating black berries, and white blossoms with the peculiar corolla split down one side and the odd ciliated indusium on the stigma. This last is one of the most singular of all the plants of the region. On the higher portions of the beaches and a meter or two back from the water-line, sea oats, *Uniola paniculata* L., will be observed, a grass about 2 meters tall, with a gracefully drooping panicle of heavy spikelets. This grows in rather close formation over large areas, forming thick tufts as it grows from season to season, and the dead culms remain clustered about the living ones.

The most important association in the *Suriana* group covering very large tracts, is formed by the bay cedar, *Suriana maritima* L., a shrub of the Geraniales order, 1 to 2 meters tall. The deep green of this shrub forms a pleasant and lively contrast to the shore plants covered with gray tomentum, as, for instance, *Tournefortia*. With *Suriana*, and often climbing up over it and hiding its small yellow star-shaped blossoms, is the beach bean, *Canavalia lineata* (Thunberg) De Candolle. A common epiphyte on the lower branches of the *Suriana* bushes is the lichen *Usnea barbata* L., with its small gray branches sticking out like a sort of a mossy covering on the twigs.

The third association is the *Chamœsyce* group, which also covers large areas on some of the keys, its members growing in situations not so suitable for the previous group. The chief component of the association is *Chamœsyce buxifolia* (Lamarck) Small. This spurge forms tracts thickly covered with its small gray-green boxwood-like leaves and tough brown stems filled with abundant latex. The rooting system of the plant is remarkable; a small individual, only 3 decimeters tall, may have a root system 9 decimeters in diameter, and were the plants growing in a soil less loose and coarse than the Tortugas sand they could scarcely be pulled up by a strong man. An ally of the *Chamœsyce* is a composite, the marsh elder, *Iva imbricata* Walter, which forms a rather tall bush, about 10 to 15 decimeters, with small, light-green succulent leaves, which have a rather pleasant bitter, acrid odor and heads of yellowish, inconspicuous flowers. A third member

of this group is a sedge, *Cyperus brunneus* S. Watson, forming conspicuous tufts of grayish foliage overtopped by the deep-brown inflorescences.

The fourth association is the *Opuntia* community. This is made up mostly of *Opuntia dillenii* (Ker) Haworth and *Paspalum cæspitosum* Flugge, a rather coarse grass about 4 decimeters tall, the branched inflorescence prolific with dark-brown, disk-shaped seeds. Frequently occurring in this association, and also to some extent in the *Chamæsyce* community, are three species common in the Tortugas: (1) the *Ipomœa pes-caprœ;* (2) its more beautiful relative, the white moon-flower, *Calonyction tuba* (Schlechtendal) Colla, which makes a most wonderful effect in the brilliant tropical moonlight with its large salver-shaped corollas starring-over the clumps of *Opuntia* or other supporting vegetation, half hidden in its enveloping heart-shaped foliage; (3) *Melanthera brevifolia* O. E. Schultz, a scrubby composite about 6 decimeters tall, bearing inconspicuous whitish blossoms, but during the hot middle portion of the day they are constantly surrounded by hosts of a tiny butterfly, *Thecla*, whose source of food is the nectar of these little flowers. Into the above four groups the predominating species of the Tortugas may be said to fall naturally on account of the influence of various factors in the environment or those inherent in the plants themselves.

## DISTRIBUTION OF SPECIES AMONG THE KEYS OF THE GROUP.

Only one other paper previous to the publication of the present one has dealt with the ecology of this region, viz, a series of maps with field-notes collected by E. O. Lansing in the spring of 1904, and published by Millspaugh in 1907.[1] This work, while fairly accurate and detailed, was compiled from notes evidently made in a very rapid survey of the islands, and in the four days (March 19 to 22 inclusive) allotted to the Tortugas group, the collector naturally overlooked many important minor features in the flora. For instance, evidence of haste is seen in overlooking the groups of sisal hemp, *Agave sisalana* (Engelmann) Perrine, among the bay cedars on Loggerhead, very old plants which were there even in the time of the third predecessor of the present light-house keeper, about 25 years ago; also on the same key numerous clumps and patches of *Opuntia dillenii* among the *Suriana* were not observed. Only one station for this plant is given for Loggerhead, viz, on the west coast near the light-house boat-shed, but the writer found it disseminated fairly well over the island in patches of old plants, often a meter high. These patches have certainly been there since the foundation of the Laboratory of the Carnegie Institution of Washington on

[1]Millspaugh, C. F., Flora of the Sand Keys of Florida. Field Columbian Museum Publication 118, Bot. Series II, No. 5.

the key in 1904, according to statements of Dr. A. G. Mayer, the Director of the Laboratory, and the aged appearance of the plants supplements his statements. But in spite of these discrepancies, the paper has been of great interest to the writer, and, as Millspaugh says in a short introduction,[1] p. 191:

"The principal value of the survey lies, therefore, first, in the historical record of the present flora, which should enable future students to determine which species have come to the different islands since 1904 and which have been unable to survive; second, in the knowledge of what species come first to such microcosms, thus forming a basis upon which to judge of the ease or difficulty of dispersion exhibited by certain species, and third, how and in what conformation species spread when brought into an untainted environment."

The paper has thus been of great value, to show what changes have taken place in the flora of the Tortugas in the twelve years which have elapsed since Mr. Lansing's survey—*i. e.*, from 1904 to 1915.

The writer spent the two summers of 1915 and 1916 at the Laboratory in the Tortugas, taking field-notes, making some physiological experiments on the plants, and working on the maps and collections of herbarium material. The herbarium specimens have all been deposited in the Herbarium of the University of Pennsylvania.

The scope of this paper has been confined to the Tortugas group because they are the most isolated of the Florida Keys and their flora is strikingly different from that of the Marquesas, 25 miles to the east, and also from that of the keys to the east of this latter atoll. The most conspicuous feature of this difference is the absence of the mangrove association to any considerable extent in the Tortugas, although Garden Key has a few well-grown young trees which in the summer of the writer's residence in the islands produced flowers and fruits. Another reason was that while the writer had the opportunity and did visit and take notes on the keys above, as well as west of Key West, the longer periods spent in the Tortugas afforded much closer observation and facilitated the securing of experimental data. His work on the other keys was largely or entirely concerned with mangroves, some physiological aspects of which have engaged his attention for several years.

The distribution of species on the various keys of the group is illustrated by maps made in the field by the author with the aid of a plane-table and sighting-rule. The outline map was made in the survey of the group in 1914 and 1915 by Vaughan and Shaw.[2] The various keys will now be taken up separately and the species illustrated by symbols on the distribution maps. A comparison is made in each case with Lansing's survey.

[1]Millspaugh, C. F., Flora of the Sand Keys of Florida. Field Columbian Museum, Publication 118, Bot. Series II, No. 5.

[2]Vaughan, T. W., and E. W. Shaw, Geologic Investigations of the Florida Reef Tract. Carnegie Inst. Wash., 1915, Year Book No. 14, p. 232.

## LOGGERHEAD KEY.

This is the largest of the Tortugas group and also the highest above sea-level and according to tradition it had in earlier times the largest stand of trees. Old fishermen (and the report was current in the times of the older light-house keepers) state that 75 or 80 years ago this

Loggerhead Key, showing buildings of the laboratory on the north end and of the light-house on the south. Walks and paths are indicated by lines. One inch = one-fifth statute mile.

island, as well as Garden Key and others of the group, supported a large stand of old white buttonwood trees, *Conocarpus erectus* L. These were largely cut down by fishermen, who occasionally camped for perhaps several weeks or months in the Tortugas; fires also are said to have had their share in devastating this old silvan flora. The central group of very old and large buttonwood trees in the parade-ground of Fort Jefferson on Garden Key is the only remnant of this supposed aboriginal silvan flora.

The booby, a kind of gannet, is said to have inhabited these islands, but has disappeared with the passing of the trees. Old fishermen relate that men, armed with clubs, would stealthily creep into the groves of buttonwood at night and kill perhaps hundreds of these birds out of pure wantonness, as they had little or no economic value. The same wanton spirit which eradicated the *Conocarpus* groves and the "boobies" in these islands has been shown by the people of the region in regard to the manatee, which is now nearly extinct in these waters; the large green and loggerhead tortoises are also fast disappearing, due to a custom of eating the eggs and killing the females. During the breeding-season of 1916 not over 6 females were reported in these islands as coming in to lay, and two of these were killed after laying and the entire settings of eggs taken, whereas even ten years ago it is said that as many as a dozen females came up on the beach in one night to lay on Loggerhead Key.

The vegetation of Loggerhead is remarkably free from the common tropical weeds when compared, for example, with Garden Key. This is probably because this island has never, since its first permanent occupation 75 years ago, been brought into frequent contact with the mainland by ships, men, or animals, except for a few months shortly after the Civil War, when a quarantine camp was established for the marines brought over from Fort Jefferson during an epidemic of yellow fever. The only permanent residents now are the keepers of the light-house; while the monthly call from Key West of the cutter of the Light-House Establishment, which rarely lasts over 2 hours at Loggerhead Key, does not seem to have served for the introduction of homovectant plants.

A glance at the distributional map of Loggerhead will show that two of the four associations mentioned above are represented in the island, the *Suriana* community predominating and the *Opuntia* association supplementing it. A photograph taken from the top of the light-house shows the vegetation to be distributed in sharply defined areas following irregular outlines. It is supposed that some of the central areas now occupied by the *Opuntia* formation (see plate 3) was cleared of the dense growth of *Suriana* by the marines and soldiers who camped there during the epidemic of yellow fever mentioned above, but the irregular outline and the isolated patches of *Opuntia* among the *Suriana* show that other agencies than man have helped to clear portions of the island.

As remarked before, the *Suriana* does not withstand a drenching of sea-water very successfully, the tomentum of the leaves holding the water until its toxic effect is produced on the leaf-tissue. The great hurricanes of the past must undoubtedly have had their share in cutting out some of the swathes in the *Suriana* community. In the list of species and on the map also some large introduced plants appear,

which add conspicuous features to the landscape and perhaps have an influence on the native flora by producing shade and conserving water, etc. Examples of these are the coconut palms, the *Casuarina* trees, the papaws, and the figs planted about the building and gardens of the light-house and laboratory; others are the *Hymenocallis*, the oleanders and *Hibiscus*, *Thespesia*, aloes, yuccas, *Pedilanthus*, and *Asparagus*. All of these, but more particularly the coconuts, papaws, casuarinas, and *Hymenocallis*, have been liberally planted about the laboratory grounds. A noticeable effect of these introduced plants was the increase in the number of plants and the size and vigor of the foliage in *Boerhaavia viscosa* when it grew under these trees or tangled among the *Hymenocallis* plants along a concrete walk leading to the wind-pump shed at the laboratory. Another example was seen in the greater luxuriance of *Chamæsyce* and *Ipomœa*, when growing near the slight shade thrown by the coconuts, the newer shoots of *Ipomœa* being more slender and tender than when growing in their accustomed habitat on the beach in fierce sunlight. These introduced plants, with the exception of the *Cocos* and *Hymenocallis*, have been brought in and planted by the Director of the Laboratory and have (plate 4) maintained themselves fairly well in such a difficult environment, although only *Casuarina* has reproduced and seeded in. This Australian plant seems to thrive remarkably in these islands. The *Hibiscus* about holds its footing when planted, but *Thespesia* and *Carica* seem to decline if not watered artificially.

An interesting point in a study of the Loggerhead flora is the comparison of Lansing's maps with the present ones. According to Lansing, the island was mainly occupied by bay cedar. Millspaugh also mentions this fact,[1] and states:

"Its central plateau, like that of Bird Key, is entirely implanted with a pure *Suriana* group, the individuals of which are about 6 feet high. The vegetation of the islet presents no association whatever, all its species being elementally scattered subtropic, maritime 'weeds.' Even the usually associated *Uniola* and *Euphorbia* [*Chamæsyce*] appear as far separated as the limits of the surface will allow."

The author is convinced that Lansing overlooked the old patches of *Opuntia* hidden in the dense growth of *Suriana*, as well as the very old groups of sisal, but aside from this the appearance of the island is much changed in the past 12 years. The spurge, *Chamæsyce buxifolia*, has not changed its position or quantity, but the *Uniola* is now found with it in its station on the northwest corner of the island as well as along the east shore, and very plentifully on the southwest shore. *Iva imbricata* seems now to have disappeared from Loggerhead. *Portulaca*, now as then, is found only around buildings both at the light-house and also at

[1]Millspaugh, C. F., Flora of the Sand Keys of Florida. Field Columbian Museum Publication 118, Bot. Series II, No. 5.

the laboratory. *Melanthera brevifolia* has migrated all along the path leading to the laboratory end of the key and has also spread into the association of *Opuntia*, while *Cyperus* and *Calonyction* occur over the central portion cleared of *Suriana*. The old grove of *Sebesten* (*Cordia*) has not changed in area or spread. *Hymenocallis* is now disseminated fairly well over the island, having been planted largely along all the walks and paths, as well as the coconuts and *Casuarina*. *Salvia serotina* is found only about the light-house, and *Capraria biflora* is not widely scattered. The shrub *Cerbera thevetia* (which has been planted for the decorative effect of its beautiful yellow blossoms) and the weeds *Poinsettia pinetorum* and *P. cyathophora* were probably introduced with soil brought from the mainland of Florida.

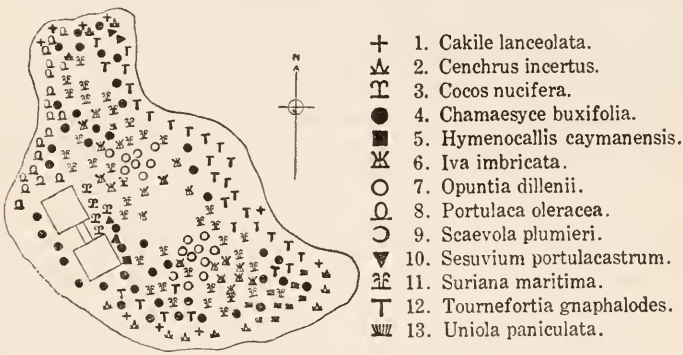
In summarizing the distribution on Loggerhead and comparing it with Lansing's account, the most conspicuous facts are the disappearance of a large amount of *Suriana* from the central portion and the spread into this area of the *Opuntia* group, the increase of *Uniola*, and the disappearance of *Guilandina* (*Cæsalpinia*) *crista*, *Iva imbricata*, and *Tribulus cistoides*. The appearance of the island is changed on account of the large number of trees and shrubs and other plants introduced for decorative and utilitarian purposes. A comparison of the lists also shows various differences in nomenclature due to synonymy, together with one systematic discrepancy, viz, *Cakile fusiformis*, as listed by Lansing and Millspaugh, is evidently *C. lanceolata* (Wild.) O. E. Schulz. *C. fusiformis*, while indigenous to the keys, has not been noted in the Tortugas. The number of seeds in the pods of the Tortugas species place it as *C. lanceolata*. The total number of species on the island at present is 41, as compared with Lansing's list of 24.

## BIRD KEY.

Bird Key, which is considerably smaller than Loggerhead, is only about 500 feet long by 300 feet broad and is now a government bird reservation for the sooty and noddy terns. These birds nest on this small island during the summer months. During the breeding-season for many years this key has been almost covered by these terns, which are now protected by the United States Government and the Audubon Society, and for this purpose a warden is stationed on the island from April to the end of August.

The writer can scarcely estimate the effect produced upon the vegetation of the island by the presence of the birds in such large numbers during the summer and in recent years of the warden, but as the birds live entirely on fish and the warden does nothing to change the physical character of the key these influences do not seem to be of great importance; but since Lansing's survey, in March 1904, a considerable change must have taken place.

Shortly after the Civil War, during the outbreak of yellow fever in Fort Jefferson on the adjacent Garden Key, Bird Key was used as a hospital site and several buildings were erected for the purpose, but we have no means of knowing what plants the key supported in that time, but it was probably during that occupation that *Portulaca oleracea* was introduced, now so prolific on the island. According to Lansing, the island was largely covered with *Suriana*, but if any plant predominates now the author would say it is *Chamæsyce buxifolia*. The *Suriana* is now confined to scattered groups in the northern and southern portions of the island. The center is occupied by masses of *Opuntia* and




Bird Key, with outlines of old hospital and Bird Warden's cottage. Two inches = one-fifth statute mile.

large quantities of *Chamæsyce* and *Iva imbricata; Cakile* and *Cenchrus incertus* are plentiful along the beaches, particularly of the eastern side. *Tournefortia* is abundant all about the edges of the inner vegetation. It seems to follow the contour of the shore, but keeps back from spray and salt mist. The eastern beach is largely crowded with the gray bushes of *Tournefortia*. *Cyperus* and *Uniola* are found most plentifully on the southeastern tip of the key, but only in tufts and small areas. Around the warden's cottage and the old hospital building are several well-grown coconut palms, which have been planted since Lansing's survey. Near the buildings also are several large clumps of *Sesuvium portulacastrum*, while *Portulaca oleracea* is particularly well scattered on the northwestern shore.

The dominant community on the key is the *Chamæsyce-Iva* association and the noteworthy changes on the island are the ascendency of this group, the decline of the *Suriana* (partly due to storms), the disappearance of *Paspalum*, and the introduction of *Iva*, *Cocos nucifera*, and *Hymenocallis caymanensis*, the latter two plants having been planted by man.

The present number of species for Bird Key is 14, as against Lansing's list of 12.

## GARDEN KEY.

This island is the second largest in the group and to a considerable extent is occupied by that antiquated, massive old brick structure, Fort Jefferson (plate 4). Almost all the history and tradition of this remote group of islands centers about Garden Key and the fort. As a fitting corollary to this, it also has the largest and richest flora in point of species of any of the keys.

Garden Key, with outlines of Fort Jefferson and adjacent buildings. Two inches = one-fifth statute mile.

A glance at the map shows that the island on the northeast side projects beyond the walls of the fort by a short arm, with the ruins of a series of coal-sheds and loading-trestles on its eastern side.

The southern side has quite a large extension outside the walls and on it are likewise ruined coal-sheds, a covered dock, and several old sheds, formerly pumping-houses, etc.; this portion also has the larger number of species. This is probably due to the fact that it is larger

than the northern projection and hence had a larger number of buildings and people on it, and also to the fact that the dock is on this southern side and all persons and commodities entering the fort passed over this strip of land to the sally-port.

The northern strip or arm of the island has a well-mixed assemblage of species, in which *Tournefortia*, *Ipomœa*, and *Canavalia* predominate, with some *Uniola*, *Scœvola*, and *Iva*. Over a tangled mass of iron rods and girders, the ruins of a loading-crane at the coal sheds, there is a luxuriant growth of *Calonyction* and several stout young bushes of *Guilandina crista*. Scattered along the western side, near the moat, are numerous *Leptilon canadense* plants.

On the eastern side of the fort, outside of the east coal-sheds on the narrow strip of soil between the moat and the beach, there was an extensive area of *Glottidium vescarium* plants, very luxuriant and of stout, tall growth. Just at the southwest corner of these eastern coal-sheds are two well-grown *Rhizophora mangle* trees, about 2 meters tall, which had flowers and fruits in 1916. On this strip also occur *Sporobolus*, *Scœvola*, *Suriana*, *Chamœsyce*, *Iva*, and a few plants of *Calonyction*.

As the southeast corner of the fort is approached, the increase in species is apparent as one gets nearer the walk leading to the sally-port. In addition to the above species, masses of *Alternanthera maritima* and *Sesuvium* are seen, together with large quantities of the rather showy blue-flowered *Valerianoides jamaicense* and the long, shining, dark-green, blade-like leaves of *Hymenocallis*. Scattered with these are *Lepidium*, *Argemone*, and *Portulaca*.

Most of the species lie to the left of the walk on going in to the sally-port. Here are numerous grasses, *Paspalum*, *Syntherisma*, *Capriola*, as well as *Uniola* and *Cenchrus*, which were likewise noted along the eastern side. *Sporobolus*, also, is fairly abundant and some of the sedge *Cyperus brunneus*. Near the old tumbled-in cistern are masses of *Calonyction*, *Hymenocallis*, *Ipomœa*, and the castor-oil plant, *Ricinus communis*, resembling trees, some being 10 to 15 feet tall, and with these many plants of *Leptilon*, *Ipomœa*, and *Iva*. Along the curving shore between the dock and the southern coal-shed were several young trees of *Thespesia* and *Suriana*. These are probably self-sown in the rather sheltered nook. Along the inner side of the coal-sheds among ballast were many plants of *Sonchus oleraceus* and *Leptilon*, which are in reality ballast plants. Stretching along the ridge of sand on the western side of the southern projection is a thick association of *Uniola* interspersed with *Leptilon*, *Cenchrus*, *Iva*, and *Canavalia*.

On the inner side, near the moat, is a mixture of *Bidens leucantha*, *Melanthera brevifolia*, *Boerhaavia viscosa*, *Scœvola*, and *Chamœsyce*. On the westernmost side of this area was found the only station for *Chamœsyce hypericifolia* in the entire Tortugas. These low-tufted, grayish plants grow thickly under several *Tournefortia* bushes.

Southwest of the southern angle of the fort are several large patches of *Opuntia* and a single *Avicennia nitida* tree. This black mangrove is the sole representative of the species on the island. Lansing mentions 30 of these trees having been planted inside the fort, but these must have perished, for not a vestige of them remains. This tree, which is about 2.5 meters tall, is probably a seedling drifted in by the waves or from seed carried in ballast from Key West. On the southern shore, near the dock, are numerous small patches of *Atriplex cristata.*

The interior of the fort has a large parade-ground (plate 4) and various buildings and ruins. This parade-ground has been planted with some introduced trees, as mentioned by Millspaugh, but a curious omission in that survey was the grove of large and old white buttonwood trees just within the sally-port. This grove is quite large and thick, and numerous young seedlings have sprung up among the older trees. While the fort was a military fortress, then during its period of use as a federal prison, later as a quarantine station and coaling-depot, and now under the jurisdiction of the naval authorities, up to date the order has been handed along that these old trees (the only remnant of the traditional forest or thickets which covered these islands) shall be untouched (see plate 4).

Notwithstanding the tendency and inclination of various care-takers of the fort to cut down and destroy all plants springing up inside the fort and the practice of burning over the parade-ground at regular intervals, and the serious fires in the fort which destroyed the large barracks and the keeper's cottage, these old trees have persisted to the present and are now strong and healthy. An interesting sport was noted in the grove, viz, a few young plants of *Conocarpus erectus* var. *sericius.* This variety probably arose quite recently as a genetical variation, very likely a mutation, as these gray tomentose trees are all quite young and have started as seedlings right in the midst of the old trees, which all have dark-green and glabrous foliage. The center of the old parade-ground is occupied every year by a thick stand of the weed *Glottidium vescarium,* which the care-taker tries to destroy by burning over the ground annually, but to no avail.

Of the trees mentioned, there are a few specimens of *Terminalia* and a tamarind (plate 5) which shows beautifully the direction of the prevailing wind by the one-sided development of the tree after it had grown so tall as to get the effect of the winds sweeping over the parapets. Here also about the buildings are several *Phœnix* palms, both *P. dactylifera* (see plate 5) and *P. canariensis,* a number of coconuts, some sea-grape trees, *Cocolobis uvifera* (which are quite old), a number of *Thespesia* trees, gum-elemi trees, *Elaphrium simaruba,* as well as *Cordia* and *Oleander* bushes. On the west side are several clumps of *Agave decipiens* (see plate 6) and in a ruined powder magazine there has sprung up, with a thicket of gum-elemi trees, a fair-sized guava

tree, which produces fruit quite abundantly, as do also the date palms and tamarind. The parade-ground is carpeted with many small native weeds, as *Boerhaavia, Bidens, Ipomœa,* etc., as well as introduced ones, *Portulaca, Argemone, Lepidium, Ricinus, Dolicholus parviflorus, Cajan cajan, Sida procumbens* and *S. carpinifolia, Phyla nodiflora, Sonchus, Leptilon,* etc.

On the earth-covered ramparts built on the top of the casemates a number of plants have secured an elevated and very dry footing. These are *Opuntia, Melanthera, Canavalia, Valerianoides, Sporobolus, Chamœsyce, Paspalum,* and *Bidens,* and in shielded crevices several good-sized trees of *Elaphrium simaruba* have managed to thrive (see plates 4 and 6).

The species listed on this interesting old key are 35, the number that Lansing and Millspaugh give for the same area—*i. e.,* for the portions outside of the fort; the parade-ground is omitted as having been too much under artificial influence to be of much importance in an ecological study; but these 35 species are not identical, for 9 of the Lansing species were not obtained in this area by the author, viz, *Amaranthus viridis, Cenchrus echinatus, Euphorbia havanensis* and *E. adenoptera, Eustachys petrœa, Heliotropum curassavicum, Sida carpinifolia* and *S. diffusa,* and *Capraria saxifragifolia,* although the last three or closely related species were found inside the fort. The 9 new species introduced into the given area are *Lepidium, Guilandina, Ricinus, Chamœsyce hypericifolia, Thespesia, Rhizophora, Calonyction, Avicennia,* and *Leptilon.* In cases of doubt concerning species, *e. g., Sida diffusa* of Millspaugh and *Sida procumbens* S. Watson, as mentioned in this paper, the synonymy could not be exactly traced, since Millspaugh did not give the authors of his species.

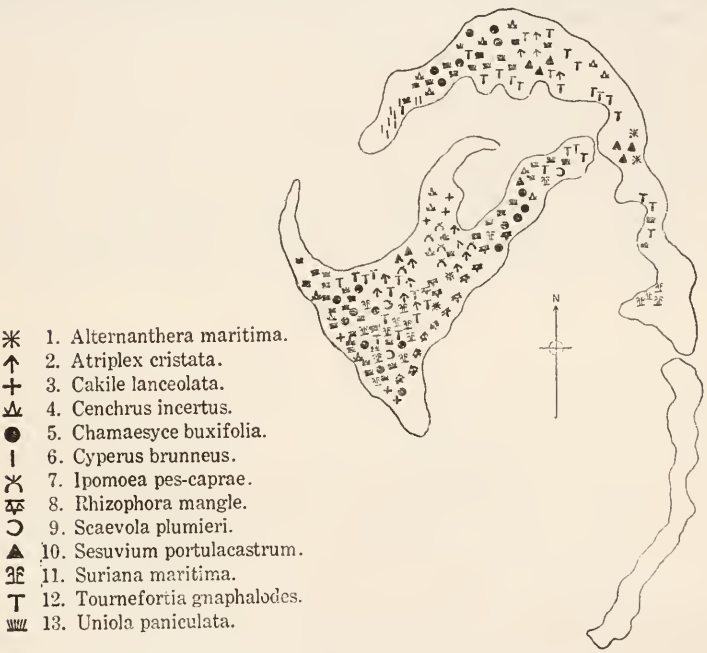
## BUSH AND LONG KEYS.

The general map of the Tortugas shows that these keys lie slightly west of Garden Key; they are very irregular and are merely narrow strips of sand and ridges of broken corals. During the winter season of 1911–12 the two keys were united by land connections due to storms, so that the outline is now that shown in the distributional map given here. The western end seems to have been the longest elevated out of the sea and supports the most vegetation. The eastern end, however, has to bear the brunt of the storms and the waves driven in by the prevailing winds, and it is perhaps for this reason that the vegetation is more scant.

Lansing and Millspaugh omitted treating this key as being "so low as to be awash during heavy weather and on this account void of vegetation." If these conditions obtained then the keys must have been built up within a year or two after Lansing's survey, since stem measurements on some of the *Suriana* and *Tournefortia* bushes on this key show them to be almost 12 years old by comparison with plants of the

same species from other keys. At any rate, the flora of the island is quite varied and well scattered. Singular as it may seem, it is on this island that more young plants of the red mangrove were found than on any other island in the Tortugas. The south shore has many small seedlings and in a landlocked tidal pool there is quite a clump of older mangroves, which are perhaps 3 or 4 years old and seem to be in a flourishing condition (see plate 6). This pool also contains a considerable school of small fish and some crabs.

This key is the main nesting-place in the Tortugas for that beautiful and graceful little sea bird, the least tern. All along the beach near the young mangrove plants one stumbles suddenly upon the pairs of



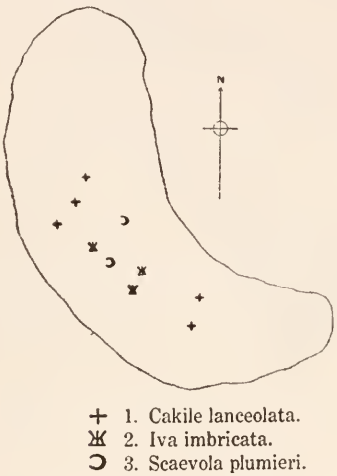

Bush and Long Keys. Two inches=one-fifth statute mile.

speckled eggs, which are very difficult to see as they lie on the bare coral sand. Later the downy chicks are just as difficult to perceive, for at the approach of a stranger they instantly become motionless balls of gray fluff. These least terns are the only birds nesting on the island.

The western shore terminates in a long and narrow northern and a broader and more rounded southern arm. *Cakile* and *Cenchrus incertus* grow along the beach at scattered intervals. Back of this and stretching east to the tidal pool is a thick aggregation of *Uniola, Tournefortia, Iva,* and a little *Suriana.* East of the pool is a sparse growth of *Atriplex, Sesuvium, Ipomœa, Cakile,* and *Alternanthera.* South of the pool and in a line with the highest tide-levels are the young *Rhizophora* seedlings. These seedlings and those about the pool were

sufficient to furnish the author with material for physiological work during two seasons at the laboratory and a large number are still left. From the middle of this island to the narrow tidal gut separating the eastern from the western island there is again a mixture of *Uniola, Tournefortia, Cenchrus, Atriplex, Sesuvium,* and a little *Scævola.* North of the portion across the inlet there is an association similar to this latter group, with the addition of *Cyperus brunneus* and *Chamæsyce* in large amount.

Following the curve of the western island as it bends south, the vegetation as plotted on the map is very sparse. It is this shore which gets the full sweep of the wind and waves from the northwest. The surface here is mostly heaps of coarsely broken corals and shells, and the




Sand or Hospital Key. Two inches = one-fifth statute mile.

Middle Key. Two inches = one-fifth statute mile.

plants it supports are a few *Sesuvium* clumps, *Suriana* and *Tournefortia* bushes, and *Cakile.* The *Suriana* is seen only on the leeward side in the more sheltered coves of the shore. In concluding the observation on these islands one can only state, in the light of Lansing's survey, which records them as barely emerged from the sea, that all the above vegetation must have appeared on them in the 12 years that have passed since 1904.

## SAND OR HOSPITAL KEY.

Stretching eastward from Garden Key and separated from each other by almost equal distances are Sand, Middle, and East Keys. All three are small and only the easternmost one, East Key, supports any real covering of vegetation. Sand Key, which is also said to have been used for hospital purposes during the yellow-fever plague of the late sixties, is only about 90 feet long and half as wide, and consists entirely of blistering and glaring white coral sand. It was visited at various

times by the author during 1915 and 1916, and at the first visit he noted near the central portion of the key one plant of *Scævola* and two plants of *Iva imbricata*. These seemed to be growing and flourishing. During July, in 1915, several visits were made and on the last occasion only one dead *Scævola* plant and several dead *Cakile* plants were found. There was nothing alive on the island but a few hermit crabs and some sea birds fishing near the beach at the western tip of the island. The sand was so hot at mid-day that, after walking over the island a few minutes, shoes had to be removed and the circuit of the island completed by wading. With this incident as an illustration, it is seen that only the hardiest plants can live on these blistering sand islands.

In Lansing and Millspaugh's paper, Lansing noted 5 species, fairly well scattered over the island—*Uniola* in the north, *Sesuvium* in three groups on the east, and *Iva* along the west shore, the central area being filled with *Ipomœa* and *Chamæsyce*. Since March 21, 1904, then, the whole island must have been denuded of vegetation and the three species noted by the author have come in lately. All the plants have gradually succumbed to the hard conditions on the island. Of Lansing's 5 species, only *Iva imbricata* was found by the author; *Scævola* and *Cakile* were not reported by him as being there at that time.

## MIDDLE KEY.

Next to Sand Key, going east, is Middle Key, the smallest of the Dry Tortugas islands. It is little more than an oval patch of sand, about 80 feet long by 50 feet wide. Millspaugh states that Lansing found no vegetation on Middle Key whatever and that it is so low that, like Long Key, it is awash in rough weather. Notwithstanding the possibility of the last statement, the author found several large tufts of dead *Cakile* on the key, its season having passed in July. It is reasonable to suppose that the island has been built a little higher in the past 12 years by the current action, and especially so since the general map accompanying the paper shows that Middle Key is built, as are indeed the others, on quite extensive shoals scarcely submerged.

## EAST KEY.

This is the most outlying key of the group since the disappearance of North and Northeast Keys a few years ago. It is the largest of the three keys stretching northeast of Garden Key and is about 4.5 miles from the latter key, about one-third of a mile in length and less than half that in width. It is almost entirely covered with vegetation and shows several associations as outlined in this paper. *Cenchrus* and *Cakile* are disseminated thickly along the shores, the latter particularly along the southeast shelf of dry sand-beach. *Uniola* and *Chamæsyce* are in fairly thick growth on the northern and southern ends, with a sprinkling of *Uniola* all along the western side. *Tournefortia*, as large,

well-grown bushes, occurs on both the east and west sides of the island, but back some distance from the shore. The northern half of the key is implanted rather thickly by two patches of *Iva imbricata*, separated by a band of *Uniola*. Near the middle of the island is a single small group of *Scævola* plants. *Sesuvium* occurs on the north and northwest shores. In a comparison with Lansing and Millspaugh's survey it is seen that the plants listed are exactly the same as those in the present survey; 8 species are given, and these are the same with the exception of *Cakile fusiformis*, which is perhaps the same systematic error noted before, *C. lanceolata* being the one noted on the island at present. Taking these facts as evidence, one may assume that in the 12 years gone by all the species have held their footing and some have increased

East Key. Two inches = one-fifth statute mile.

in amount, but not at the expense of the others, and as this key is very rarely visited, the ecologic influences governing the distribution of the species have been undisturbed.

## SPECIAL ECOLOGY.

*Seasonal differences.*—As might be expected from the data presented under "climate," the conditions are fairly uniform. The general appearance of the islands is the same at all seasons of the year. Of course during the winter months and early spring, after the heavy rains in September to December, there is more green carpeting in dry places, due to various grasses and low herbs which turn brown and dry in the later and hotter summer months, and such tropical trees as the

large *Ficus hispida*, planted in the courtyard at the light-house on Loggerhead Key, drop their leaves during the coolest months, December and January. But this dormant condition lasts only a few weeks; other plants, as the *Hibiscus* and oleanders, seem to bloom and flourish throughout the year, and during the summer months particularly are covered with showy crimson, scarlet, and pink blossoms.

*Flowering and fruiting.*—These phenomena are not definitely limited in the Tortugas region. Coconuts frequently bloom and ripen at the same period, and the same is true of the geiger-trees, some of which have showy clusters of scarlet flowers and bear on the same branch the hard, pointed, white fruits. The *Scævola* often bears its white blossoms simultaneously with the large edible-looking but nauseating black berries. Some periodicity, however, has been noted in the red mangrove and the sea-grape, *Cocolobis uvifera*. Trees were seen with blossoms and ripe or nearly ripe fruits, but never trees with blossoms together with very immature or half-ripe fruits and fully ripened ones. There must be some definite cycle of growth which prevents the occurrence of fruits at all stages in these trees.

Herbs, such as *Melanthera*, *Valerianoides*, and *Alternanthera* have buds, blooming inflorescences, and old dead and dry flower-clusters all on the same plant; other herbs, such as *Cakile* and some of the grasses, have a well-defined growing-season. *Cakile* grows only during the winter and spring; by June the plants are full of ripe seeds, and during July the plants die and become tumble-weeds. *Tournefortia* and *Suriana* seem to have cycles of growth not separated by long periods, for some individuals are frequently seen having flowers and ripe seeds. The Convolvulaceæ, represented by *Ipomœa* and *Calonyction*, appear to have all stages of flowers and fruits, for even long periods of drought do not seem to prevent *Ipomœa pes-caprœ* from producing its showy rose-purple funnels along the runners trailing 20 to 30 feet across the burning white sand-beaches.

*Influence of soil.*—There is not much field for observation under this head, since the islands are essentially all alike geologically—*i. e.*, the soil is all white calcareous sand, but at several places in the Tortugas there is a slight variation in the soil. On Bush Key, near the small tidal pool, the soil is lower than the adjacent sand and various unicellular and a few filamentous algæ (*e. g.*, *Lyngbya*), etc., grow among the mangrove seedlings. In similar situations on Boca Grande the writer observed *Sesuvium*, *Alternanthera*, and *Batis maritima* in salt meadows or marshes where young rhizophoras were also establishing themselves. However, on Bush Key only an algal flora was observed on the surface of the soil and on the mangrove stems.

The other variations in soil were due to artificial conditions. On Loggerhead several carloads of soil had been brought from Maplewood, New Jersey, and this supports a few introduced weeds, such as

*Syntherisma* and *Cenchrus echinatus*, with several *Poinsettias*. On Garden Key portions of the parade-ground, possibly through long years of cultivation and some attempts at fertilization and artificial watering, show a difference in the soil from that of the rest of the key. The accumulation of some humus here also makes a change in the soil's character. This portion of the parade-ground is thickly covered with a mat of *Lippia*, various examples of *Sida*, *Dolicholus*, etc., plants which need slightly more nutriment in their substratum than is afforded by the coarse, limy gravel and sand of other parts of the key.

*Human and animal influence on vegetation.*—Man's influence on the plants in the Tortugas may be designated as constructive and destructive. The introduction of plants for use or ornament on Loggerhead and Garden Keys and their introduction unwittingly with ballast, etc. (such as *Leptilon*, *Sonchus*, *Syntherisma*, *Portulaca*), together with coconuts, papaws, *Casuarinas*, and *Salvia serotina* (used in earlier years as a febrifuge), may all be classed as constructive influences. The cutting down of the white buttonwood trees by the old fishermen, according to tradition, the burning off of the *Suriana* on Loggerhead, and the burning over of the parade-ground in the fort on Garden Key are destructive activities. On Bird Key the presence of the warden does not seem to have produced any change in the vegetation, while the terns which breed on the island have very little effect, as they do not feed on any plant substances and it is only the noddy terns which make nests of a few dry sticks; the other two species of terns lay their eggs on the bare sand.

Millspaugh ascribes to birds a large influence in the distribution of plants in this region, but in the writer's opinion this has been overestimated; the only birds in the region are the terns and a few frigatebirds which prey on the terns. None of these birds are waders, nor do they spend much time on land, according to the author's observation. Millspaugh mentions 8 plant species as avevectant by the feet of sea birds, six of these occurring in the Tortugas, but as there are few birds in these islands and those are of such habits as scarcely to permit of carrying seeds in the webbed-toe expansion, the hypothesis is hardly tenable. A more reasonable factor for distribution in the Tortugas is the sea alone. The undoubtedly aquavectant plants (as *Cakile*) appear on the islands no sooner than such supposedly bird-borne plants as *Cenchrus* and *Scævola*.

Other animals associated with plants are the red land-crab, *Gecarcinus lateralis*, which lives on various islands, but was observed especially on Loggerhead, where it fed on decaying leaf-mold accumulating in the grove of *Sebesten* trees, but it probably has no effect on this tree's economy. A small black beetle also lives in this tree's deep salver-form corolla and perhaps aids in fertilization. Another insect is the tiny butterfly *Thecla*, which lives on the nectar of *Melanthera* and incidentally pollinates its stigmas.

*Storms.*—Hurricanes and great waves driven by continuous winds have wrought more havoc on the vegetation of the Tortugas than perhaps any other agents. Whole keys have been washed away by some of the great storms, and islands have been completely denuded of vegetation. Not only on these sand islands, but in the mangrove swamps of larger islands (as at Boca Grande), large areas of swamp were dead and piled up densely with the decaying branches of shattered *Rhizophora* trees. To storms also may be laid some of the destruction of the *Suriana* on Loggerhead and Bird Keys by driving in the salt spray, which kills the bushes, or by the mechanical injury of undermining the roots by high waves and later leaving the absorptive system exposed to the drying air. This latter case is observed on the eastern shore of Loggerhead, where the bank was eroded and long ridges of the *Suriana* were dead, with their roots sticking up in the air.

*Structure in relation to environment.*—This subject is well illustrated in the Tortugas. All the plants of these dry islands, in which there are no springs of fresh water of any sort and where the substratum is of a loose, porous nature, must be adapted to conserve moisture. The structures facilitating conservation of moisture in the Tortugas flora are various. In *Tournefortia* and *Suriana* the leaves are densely covered with tomentum and pubescence; they are spatulate in shape, which permits their being set closely together, and as a further reaction they assume an appressed hyponastic position during the middle portion of the day or in prolonged droughts. *Scævola* and *Ipomœa*, both of which have large leaves, are heavily cutinized and frequently have sunken stomata; they also assume the hyponastic appressed position in unfavorable conditions and seasons. *Chamæsyce* has small, reduced leaves, heavily cutinized, appressed, sessile, and flap-like, which transpire very slowly. *Iva* has glabrous, heavily cutinized leaves with thick, fleshy mesophyll, containing water-storage tissue. *Cenchrus*, *Cyperus*, and *Uniola* have narrow, reduced leaves with small stomata and, together with many grasses, roll inward during dry seasons or in dry situations, the reaction being due to the thin-walled water-storage cells in the sinuses of the delicate ridges losing water, the lowered turgescence causing the leaf to involute.

A peculiar reaction to environment was noted in the *Poinsettias*. Individuals of species occurring in the Tortugas were found in more favorable situations on the mainland of Florida with rather broad blades; with variations in environment and decreasing moisture and shade, all stages were seen, down to leaves which were little more than midribs. *Boerhaavia* has a rather broad blade, but is protected from excessive transpiration by tomentum and glandular hairs. Thus it is seen that on minute examination nearly every plant in this region has some special protective feature to guard against loss of water, the acme being reached, of course, in *Opuntia*, which has no leaves whatever, a thickly cutinized epidermis, and mucilaginous sap.

In this connection the actual transpiration records taken by the writer with a potometer in many of the representative plants of the Tortugas prove very illuminating. The records were taken in both sun and shade and are given in condensed form in the table following:

*Potometer transpiration-rate averages.*

| No. | Species. | Weight. | Quantity. | Length of time in sun. | Length of time in shade. |
|---|---|---|---|---|---|
| | | *gm.* | *c.c.* | *h m* | *h m* |
| 1 | Suriana..... | .6 | 1 | 1 15 | 1 |
| 2 | Chamæsyce... | 3.7 | 1 | 1 50 | 2 10 |
| 3 | Canavalia.... | 9.1 | 1 | 22 | 40 |
| 4 | Tournefortia.. | 3.5 | 1 | 10 | 12 |
| 5 | Ipomœa..... | 3.6 | 1 | 1 25 | 37 |
| 6 | Boerhaavia... | 4.5 | 1 | 36 | 25 |
| 7 | Scævola..... | 7.5 | 1 | 13 | 25 |

It is seen that some plants have transpired the given quantity of 1 c.c. in a shorter time in shade than in sun. These are *Suriana*, *Ipomœa*, and *Boerhaavia*. This apparent contradiction of the law of transpiration, which expresses the fact that the higher the temperature the greater the water transpiration, is explained by the fact that in the intensely hot sunlight and the reflection and brilliant glare of the white sand those plants were heated beyond the point at which transpiration was at a maximum and the leaves lost so much turgescence that they wilted and became flaccid, with an almost complete inhibition of transpiration. This phenomenon is observed more particularly in young tissue, as tender shoots and branches which still have collenchyma in the stems and poorly developed epidermis on the young leaves. It was necessary to use such shoots of the three above-mentioned plants, since the older and more woody stems could not be fitted into the small Ganong potometer. However, this reaction was noted in plants growing *in situ* just as well as in the potometer subjects.

In several patches of *Boerhaavia* along a walk at the laboratory it was noted that during hot days, from before noon to mid-afternoon, the younger shoots would be hanging limp and flaccid, while about 4 p. m. they would assume their wonted erectness with turgescent leaves. Plants in more northern climates also frequently show this; notably *Dahlias* planted in open sunny places have often been observed by the writer to have all the upper leaves completely wilted in hot August weather during the middle portion of the day, while with the approach of evening they completely recovered. This temporary loss of turgescence may occur daily without apparent injury to the plants.

Of all the plants tested, *Chamæsyce* seems the best protected and transpires the given quantity in the longest time. *Suriana* and *Ipomœa* come next, while *Tournefortia* with its dense silky tomentum and *Scævola* with thick fleshy leaves heavily cutinized show relatively little

difference in the rates in sun or shade conditions and actually give off a cubic centimeter of water in a very short period—*i. e.*, in about 14 minutes. It is thus seen that this physiological action of loss of water varies considerably, even in these plants adapted to these xerophytic conditions and highly specialized morphologically.

## MARINE ECOLOGY.

The submerged plants growing about the Tortugas are not many, since marine algæ most abound on rocky shores and rocks are conspicuously lacking in the Tortugas physiography. Of the higher plants several interesting spermatophytes are very abundant, viz:

(1) *Thalassia testudinum* Köenig and Sims, which occurs on extensive areas in shallow water. The leaves and stems of this plant, the turtle-grass, are cast up in long rows by the waves, particularly after storms, on the sandy beaches of the islands.

(2) Another component of this mass of débris is the manatee-grass, *Cymodocea manatorum* Ascherson, which has much more slender leaves and a peculiar inflorescence. It was the author's good fortune to secure both of these plants in bloom, and the *Cymodocea* in fairly large quantity by going down in a diving helmet in about 3 to 4 meters of water and walking about on the bottom, making a close observation of the beds of this grass. Algæ were also collected in the same manner.

(3) Two other spermatophytes, which were obtained by the deep-sea dredging apparatus carried by the Laboratory yacht, were two species of *Halophila*, growing in 17 to 19 fathoms of water out in the Gulf Stream. These were *H. engelmannii* and *H. baillonis* Aschers. The occurrence of these plants in this locality and their interesting relations to the region have been discussed by the writer in another paper.[1] These and the calcareous algæ which are given in a list below are quite abundant. Representatives of the Rhodophyceæ and the Phæophyceæ are not nearly so plentiful. The *Udotea* and *Penicillus* are quite common in sandy shallows and various species of *Halimeda* contribute a large share to the detritus making up the land. *Codium* and *Acetabularia* are frequent on rocks, shells, or other submerged objects affording a firm foothold. *Gracillaria* is mostly brought up on shells and sponges in the dredges along with species of *Halophila*, while *Sargassum bacciferum*, and occasionally *Valonia*, *Dictyosphœria*, *Lyngbya*, *Hypnea*, and *Lawrencia*, drift about the islands and in the Gulf as large mats or rafts. These are washed up on the shores in long windrows, and while floating these mats of *Sargassum* furnish an abiding-place for numerous small animals, especially several species of crabs. One which is fairly common matches exactly the yellow-brown fronds of the *Sargassum* and can be seen only with difficulty in a tangle of the gulfweed when thrown into an aquarium.

[1]Bowman, H. H. M.: Adaptability of a Sea Grass. Science, n. s., vol. XLII, 1103, pp. 244–247.

*List of Submerged Spermatophytes and Algæ in the Gulf of Mexico about Tortugas.*

ORDER NAIADALES.

*Cymodocea manatorum* Ascherson. Manatee-grass.

ORDER HYDROCHARITALES.

FAMILY ELODEACEÆ.

*Halophila engelmannii* Ascherson.
*Halophila baillonis* Ascherson.

FAMILY HYDROCHARITACEÆ.

*Thalassia testudinum* Köenig and Sims. Turtle-grass.

ALGÆ.

CYANOPHYCEÆ.

*Lyngbya majuscula* (Dillwyn) Harvey.

CHLOROPHYCEÆ.

*Caulerpa sertularioides* (Gmelin) Howe.
*prolifera* (Förskal) Lamarck.
*racemosa* (Förskal) Agardh. var. *occidentalis* (J. Agardh.) Börgesen.
*ashmeadii* Harvey.
*crassifolia* (Agardh.) J. Agardh.
*Codium tomentosum* (Hudson) Stackhouse.
*Penicillus dumetosus* (Lamarck) Decaisne.
*Udotea flabellum* (Ell. and Sol.) M. A. Howe.
*cyathiformis* (Decaisne) Howe.

ALGÆ—continued.

CHLOROPHYCEÆ—continued.

*Halimeda simulans* M. A. Howe.
*tuna* (Ellis and Solander) Lamarck
*tridens* (Ellis and Solander) Lamarck.
*opuntia* var. *minor* (Ellis and Solander) Lamarck.
*Valonia ventricosa* L.
*Dictyosphæria favulosa* (Agardh.) Decaisne.
*Acetabularia crenulata* Lamaroux.

PHÆOPHYCEÆ.

*Dictyopteris justii* Lamarck.
*Zonaria lobata* A. K. Agardh.
*Padina pavonia* (L.) Gaillon.
*Sargassum natans* (L.) Meyer—*S. bacciferum*.

RHODOPHYCEÆ.

*Hypnea muscoformis* (Wulfen) Lamarck.
*Acanthophora spicifera* Vahl, *A. thierii* Lamarck.
*Lawrencia obtusa* (Hudson) Lamarck.
*Galaxaura flagelliformis* Kjellman.
*Wurdemannia setacea* Harvey.
*Corallina rubens* L.
*Gracillaria confervoides* (L.) Greville.

## CONCLUSION.

In this treatment of the species in the Tortugas it has been aimed to give some idea of the character of the dry-climate plants inhabiting these islands, their distribution, and particularly the changes which have occurred on the various keys since Lansing's survey, with an attempt to analyze the reasons for such changes. This, it is hoped, has been done, with the help of herbarium specimens collected and living plants sent north to the University of Pennsylvania Botanical Garden, and also the extensive field-notes and laboratory experiments made by the writer during his residence of two summers in these islands.

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1. Beach terraces on Loggerhead Key showing *Suriana maritima* in background, runners of *Ipomoea pes-caprae* and *Tournefortia gnaphalodes* in foreground.
2. Beach on Loggerhead Key showing *Uniola paniculata*.

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3. Large area on Loggerhead occupied mostly by *Opuntia dillenii*.
4. Pure stand of *Tournefortia gnaphalodes* with several plants of *Hymenocallis caymanensis* in the foreground.

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5. View of Loggerhead from the top of the Lighthouse looking north-east. Dark areas occupied by *Suriana* and lighter ones by *Opuntia* and *Calonyction*. Laboratory buildings near extreme point.

6. View of Loggerhead from top of Lighthouse looking south-west. Dark areas *Suriana* and lighter ones *Opuntia, Ipomoea, Paspalum, Cyperus, etc.* Cocoanut palms in lighthouse enclosure in foreground.

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7. Old Fort Jefferson on Garden Key. Vegetation is shown growing high up on the earth-covered ramparts and bastions.
8. View of Parade Ground in Fort Jefferson showing *Sebesten* bushes. Inflorescence of *Agave*, Guavas and Gum-Elemi bushes in the background.
9. Grove of ancient *Conocarpus* trees in the Parade Ground at Fort Jefferson, a remnant of the traditional, original, silvan flora of the Tortugas.
10. Plant of *Hymenocallis caymanensis* in bloom.

11

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11. Coconuts and old Tamarind Tree in Parade Ground illustrating the direction of the prevailing wind.
12. Oleanders and *Phoenix dactylifera* bearing clusters of dates in Parade Ground at Fort Jefferson.

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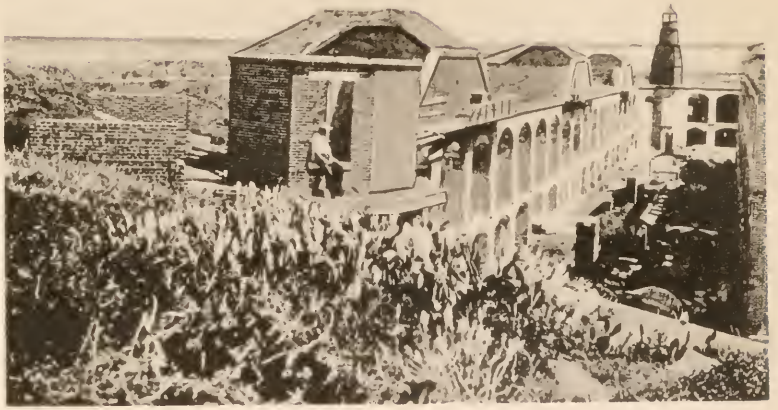

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13. Young mangrove seedlings on the beach at Long and Bush Keys.
14. *Opuntia dillenii* growing high on the ramparts at Fort Jefferson.
15. Inflorescence and plants of *Agave decipiens*.
16. Gum-Elemi Tree, *Elaphrium simaruba*, growing in a crevice of the parapet at Fort Jefferson, Garden Key

VI.

# THE ORIGIN OF THE ELECTRIC ORGANS IN ASTROSCOPUS GUTTATUS

By E. GRACE WHITE

Seven plates, one text-figure

# THE ORIGIN OF THE ELECTRIC ORGANS IN ASTROSCOPUS GUTTATUS.

By E. Grace White.

## INTRODUCTION.

Living organisms, aside from expending energy in the growth, differentiation, and reproduction of their bodies and in secreting many substances useful in the preservation of their lives, may also release energy in the form of motion, electricity, heat, and light, all of which may play a more or less important part in the maintenance of life. Of these powers, that of producing electricity specifically and in quantities large enough to be of use to the organism is confined to seven groups of fishes, two of which are elasmobranchs and five teleosts. The same power has been reported to be present in a snail and in some insects, but these reports have not been confirmed. It seems clear that among the fishes the power to produce electricity has been developed independently in the seven groups mentioned. All the activities of cells, such as secretion, motion, or nerve-conduction are accompanied by the release of a very small amount of electric energy, which apparently can not be of any possible use to the animal. Are the powerful electric discharges, sometimes over 100 volts in strength, which occur in these seven groups of fishes the result of evolutionary processes that first took their origin in the very minute electric discharge of the ordinary forms of tissue-cells?

A beginning to an answer to this question may be made by studying the structure of the electric organs, and particularly their morphological and cytological development in the ontogeny of the forms. This the writer has attempted to do, as suggested by Professor Ulric Dahlgren, of Princeton University, in the case of the remarkable electric organ of *Astroscopus guttatus* and *Astroscopus y-græcum*. I wish here to express my gratitude to Professor Dahlgren for his generous offer of the material, for his kindly direction of the problem, and for his most valuable criticisms. I wish also to thank Professor E. G. Conklin, of Princeton University, and Professor E. B. Wilson, of Columbia University, for reading and criticizing the paper. The expenses of collecting the material for this work were met by donations extending over a series of years from the Carnegie Institution of Washington, through the kindness and interest of Dr. A. G. Mayer.

## HISTORICAL SURVEY OF THE SUBJECT.

### GENERAL.

The power of certain fishes to give electric shocks has been known from the earliest times. A hieroglyphic representation of *Malopterurus electricus*, the electric cat-fish, has been preserved on the Egyptian tomb of Ti (Gotch 50), and the still more formidable shock of the electric ray of the Mediterranean was used by the Roman physicians as a charm to cure their patients, procuring for the fish the popular and familiar name of torpedo (Dixon 38). The numbing power of *Gymnotus* has long been feared by the South Americans, and many accounts of the extraordinary behavior of this giant eel-like fish have been published from time to time in popular form (Gotch 50). Rumor would extend this extraordinary power to the snail *Daudabardia*, and General Davis describes the "wheel-bug" of the West Indies, *Reduvius serratus*, with electric organs in its legs (Dixon 38), but these reports have not yet been substantiated.

The seven groups of fishes which have this electric power represent a wide range in structure and environment. *Torpedo* and the Rajidæ are marine elasmobranchs and are of very similar structure, being broad, flat, of slow motions, with a habit of lying on the bottom of the ocean. *Torpedo* is especially common in all warm seas, but the skate has been found much more widely dispersed in the salt water of the world. *Malopterurus*, *Gymnotus*, and the Mormyridæ are fresh-water teleosts. *Malopterurus* differs considerably from the other two groups in structure, being a silurid of considerable size. It inhabits the River Nile. *Gymnotus* is a South American eel-like fish of great length, found abundantly in the South American rivers. It has the characteristic eel-like method of locomotion. The Mormyridæ are typical teleost fishes of great variety of shape and difference of habit, abounding in the Nile and other fresh waters of Africa (Gotch 50).

Although the numbing effects of these fishes have been known so long, the cause remained a mystery until in 1773 Dr. Walsh (92) discovered the presence of "intense electrical currents" in *Torpedo*, "developed through the functional activity of special organs situated, on each side, in the lateral mass of the body of the fish." In 1835 a description of the electrical organs of both *Gymnotus* and *Torpedo* appeared in the works of J. Hunter (63), while in 1844 Stark (87) and in 1846 Robin (78) described similar organs on either side of the spinal column in the tail of *Raja*, although no shock could be felt by the hand. From that time the literature on the subject has constantly increased until now every branch has been covered. The majority of the investigations were carried on during the latter part of the nineteenth and early part of the twentieth century, but a few investigators have continued the study to the present day.

## STRUCTURAL.

The general structure of the organs in *Torpedo* had been described in 1678 by Lorenzini (70), and a detailed account was published in 1835 by John Hunter (63), but the anatomy of the electric organs in general was not given much consideration by investigators until the discovery, by Bilharz, in 1857 (16), of the electrical plates in *Gymnotus*. Ballowitz worked out the fine anatomy of the electric organs of *Torpedo*, *Gymnotus*, and the Rajidæ, to the latter of which he gave the name of the "pseudoelectric fishes," and to the organs the name of the "pseudoelectric organs," inasmuch as their structure resembled that of other electric organs, while their function was not then known. Ogneff (75) and Max Schultze (85) made careful and accurate observations of the innervation of these organs and of the finer details of the nerve-endings of the same.

The peculiar structure common to all electric fishes is the semitransparent material, of the consistency of jelly, which lies between and around the electroplaxes and in which lie the connective-tissue septa and numerous nerve-branches. In *Torpedo* these are two large masses, concave on the inner border and divided by septa into hexagonal columns, the ends of which lie under the dorsal and ventral surfaces of the skin. In *Torpedo occidentalis* there are 1,969 columns, in *Torpedo ocellata* but 450 (Gotch 50).

In *Raja* there are two very slender organs, tapering at both ends and lying one on each side of the spinal column. These organs are formed from and lie embedded in the muscles of the tail.

In *Gymnotus* there are four such organs, two dorsal and two ventral, of which the dorsal are the larger. The organs are divided into columns which run variable distances from the cephalic end to the tip of the tail of the fish, which may be from 8 to 10 feet in length.

*Mormyrus* has four organs formed from and replacing the posterior regions of the muscles of the tail. The long diameter is parallel to the spinal column, and with the general position very like that of the organs in *Gymnotus*, though not extending so far into the anterior end of the body. In *Gymnarchus* there are eight cylindrical organs, four on each side, embedded in the muscle-tissue of the tail, as close to the median bony parts as a little connective tissue in between will permit.

The organ of *Malopterurus* is peculiarly situated in the thickened skin and is imperfectly divided into halves by a connective-tissue septum on the ventral surface. It enwraps the whole body except the fins and the head.

The finer anatomy of the electric organs differs considerably in the different groups. In *Malopterurus* there is no obvious arrangement into columns, the organ being composed of lozenge-shaped electroplaxes, dove-tailed into each other and surrounded by the characteristic jelly-like material. Each half of the organ is innervated by a

single gigantic nerve-cell, with but one axis cylinder, the branches of which reach all of the somewhat over 72,000 compartments in each half of the organ and are estimated to have a peripheral distribution unsurpassed by that of any other single nerve-cell (Gotch 50).

In all the other electric fishes the organs are divided into columns, themselves subdivided at regular intervals by connective-tissue septa and fixed at their peripheral edges by the boundary wall. Each of these compartments contains a protoplasmic mass, the electroplax, in which the efferent nerves end, while the rest of the space is occupied by the transparent material. The essential elements are much the same in all. The protoplasmic mass with its supporting fibers, cross-striations, and nerve terminations is called the electric plate, electric disk, or electroplax. The nerves on coming in contact with the electroplaxes branch in a characteristic dichotomous manner in most of the groups.

In *Raja batis* a band of parallel wavy fibers crosses the transparent area, still possessing the optical properties common to ordinary striated muscle-fibers and representing the vestiges of the cross-striation of the voluntary muscle-fibers, from which, according to Ewart and Engelmann (39 and 41), the electric plate has been derived. This layer will be termed the striated layer for convenience in this paper, although the striations are no longer wholly comparable to those of muscle-tissue and although they have almost entirely disappeared in *Gymnotus* and *Torpedo*, the strongest of the electric fishes. In *Torpedo* there is a faint fibrillation in each electroplax during its early embryonic state, which is completely resorbed during development. In *Gymnotus* and in *Malopterurus* no indication of the striations is visible even in the earliest stages yet seen. It is therefore evident that the loss of definite striation is correlated with the gain in electrical power and it is possible that the evolution of the electric organs may follow the loss of the original muscle striations.

## PHYSIOLOGICAL.

Perhaps the best-known of all the investigators of electric fishes is DuBois-Reymond. The founder of electro-physiology, he has exhaustively covered the subject of electrical currents in muscle, nerves, and electrical organs, carrying on, in the early eighties, a prolonged dispute with Hering (57) and Hermann (58, 59) concerning the extent of polarization arising in a muscle when an electrical current has been passed through it. DuBois-Reymond experimented on living *Malopterurus* and on living *Torpedo* in Berlin, and under his direction Sachs worked on living *Gymnotus* in South America. Their combined results are so comprehensive and so accurate as to leave room for no further investigation of the same nature, and the name of DuBois-Reymond is recognized to be that of the leader in the physiological researches on animal electricity.

Cavendish in 1780 (29) was the first to conceive of the idea of current-curves and to imitate the shock of *Torpedo* by ordinary electricity. He was far in advance of his time and it was not until a century later that Faraday (42) reached the same opinion. Although it has since been possible by modern methods and apparatus to considerably modify and correct the current-curves of Cavendish, the basic idea remains his.

In 1831 Colladon of Geneva, experimenting on the *Torpedo,* gave the name of "Colladon's currents" to those currents running between points on either the ventral or the dorsal surface (31). A few observations were made the same year by Matteuci (72), but not until the discovery by Bilharz in 1857 (16) was any further advance made in the study of the electrical currents. DuBois-Reymond then calculated that "the greater the length of a *Torpedo* column, provided the number of plates in the unit of length is the same, so much greater must be its electromotive force; and by as much as the columns diminish in height from the inner to the outer edge of the organ, by so much may the electromotive force of the median columns be greater than that of the outer ones" (18). At the same time he discussed the matter of immunity in electric fishes, finding that all electric fishes are practically immune to their own shock and relatively so to the shock of another fish of the same species, much as a viper is immune to its own poison, in spite of the fact that the body of the fish is much more favorably placed to receive the shock than are the bodies of neighboring fishes. Definite electric currents are known to pass through the body of the fish. They have been detected in the digestive tract, in the brain and spinal cord, and found to be of appreciable intensity, yet the fish remains apparently unaware of the shock.

Marey in 1879 (71) was the first to represent graphically the reflex currents of *Gymnotus* and *Torpedo* by the use of the telephone. Schönlein (83) repeated the experiments with a galvanometer and calculated the voltage of the individual electroplaxes in *Torpedo* and in *Raja;* Cremer (Gotch 50) used the "saitenelektrometer" of his own invention, and in 1899 Garten (48) made very accurate measurements and records with the capillary electrometer. In 1881 Sachs (80) published his work on the physiology of the organs of *Gymnotus;* while Gotch and Burch (52, 53) and Koike (66) have independently published similar works on *Malopterurus,* so that the shock in these three fishes has been exhaustively investigated. The general results have shown that electric organs have much the same electrical properties as muscles and nerves, with the difference that in the case of the electric organs the elements are considerably modified and so arranged in series as to give the effect of a battery in which an otherwise insignificant current can be made measurable by addition (Gotch 50).

Gotch and Burdon-Sanderson (27, 28) followed up these experiments on the weak electric fishes, finding them to be similar in both the

Rajidæ and the Mormyridæ to those of the strong electric fishes, except in the intensity of the shock. The true electrical nature of these organs, which had been previously considered electrical from their structure but had not been determined by experiment as to function, was now ascertained, for definite electrical currents could be detected by the galvanometer.

The combined results of these investigators, notwithstanding certain prolonged controversies, have led to a pretty definite agreement as to the nature of the activity of these organs. The activity of the electric organs is dependent upon the arrangement of the electrical plates in a linear series for its adequate expression, and the columnar structure of the organ thus modifies rather than determines the characteristics of the activity. The nature of these activities lies in the electrical change in the nerves themselves, expressed through the agency of the electroplaxes. That the disk is the excitable structure responding to impulses from the nerves is an abandoned theory contradicted by all experimental evidence, for such paralyzing drugs as atropin and curare, which are known to effectively destroy the action of muscle-tissue, have no effect upon the activity of the electric organs unless given in such doses as to paralyze the nerves themselves. All the effects in the electrical organs are connected with excitation, and its concomitant alteration, which is always accompanied in the nerve by rapid electric changes, while the structural nature of the organ is such that the changes in each group of nerve terminations may become conspicuous by summing with those of the neighboring groups (Gotch **50**).

Another law which has been generally accepted is that of Pacini, in connection with the probable direction of the current in the different electric fishes. He states that the electric current will run from the electric layer where the nerve-endings are, to the nutritive layer, so that the electric surface will be negative to the nutritive one. Experiment has so far verified this law in every case which has been examined in this regard, except in that of *Malopterurus*, in which the current goes in the opposite direction, namely, from the nutritive to the electric layer.

## EMBRYOLOGICAL.

In 1877 Babuchin (**4**), in 1888 Ewart (**40**), and in 1894 Engelmann (**39**) worked out the origin of the electric organs of *Torpedo* and the Mormyridæ, then known as the pseudoelectric fishes, showing that, in general, electric organs have arisen by the modification of certain striated muscle-cells. In *Torpedo* and the Rajidæ each electroplax arises from a single cell, but Babuchin has shown (**2**, **3**) that in the Mormyridæ a syncytium of cells from the fibers of the sacrolumbalis muscles may go into the formation of one electroplax. Dahlgren has shown that each electroplax probably arises from the union of all the muscle-fibers in one myotome. It was in the midst of these researches

that Babuchin (2) came to the conclusion that, inasmuch as the origin, structure, and functional activity of the pseudoelectric organs, although diminutive and less highly differentiated than those of *Torpedo* and *Gymnotus*, nevertheless are fundamentally the same; therefore, "Es existieren keine pseudoelektrischen organe, es gibt nur grosse und starke, kleine und schwache elektrische organe." The term pseudo-electrical organs has since been definitely abandoned and the Mormyridæ and the Rajidæ are known as the weak electric fishes.

In 1880 Fritsch (44) described in detail the electric organs of *Malopterurus* and startled investigators by attempting to show that the electroplaxes were neither arranged in parallel series, as in all other electric fishes, nor derived from muscle-cells. He tried to prove that the organs in this fish are developed from certain gland-cells in the skin, an observation which aroused much discussion and which never has been substantiated. No investigator has been able, on the other hand, to prove the origin of the organs from any of the muscle-cells, so the matter remains an open question to this day, with a possibility of thus bringing *Malopterurus* into line with the other electric fishes. The peculiar structure of the electroplaxes, however, and the inability to harmonize the direction of the current with Pacini's law are facts which can not be denied, and *Malopterurus* stands as the great exception to the general rules for electric fishes. At any rate, *Malopterurus* has not sacrificed any of its motor muscles to the formation of the organs and its movements are not in any way hampered, while the electric coat, which completely surrounds the body, forms an effective protection as well as a means of easily capturing its food. *Gymnotus* and *Torpedo*, on the other hand, move so slowly that they have to numb their prey at some distance and then follow them up at their leisure. It is doubtful whether the weak electric fishes use their electric organs for either protection or for capturing food, although it is possible that they may capture in this way small crustacea and other minute invertebrates.

Recently Professor Dahlgren has become interested in certain American species of electric fishes. He has published several papers, one on the anatomy and muscular origin of the electric organ of *Gymnarchus* (32), an African form distantly related to the Mormyridæ, and several on the gross anatomy and habits of the star-gazer, *Astroscopus* (33, 34, 36), a marine teleost of the toad-fish group, a group hitherto unrepresented among the electric fishes. In 1906 Dahlgren (36) and Silvester published an account of the adult *Astroscopus*. The authors had been interested in reports from Charles H. Gilbert and J. A. Henshall (Jordan 64, 65), who reported having felt shocks from the two species *Astroscopus guttatus* and *Astroscopus y-græcum*. Fishermen who were interviewed said that they had always known of the numbing power of these fishes and had often received shocks from stepping on them as they lay buried in the sand.

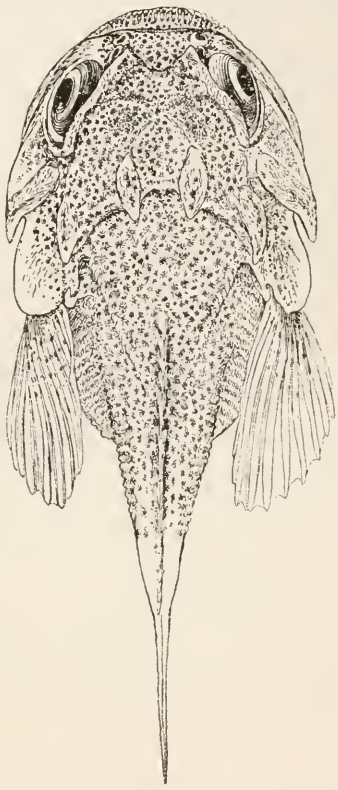
The organs of *Astroscopus* form two irregular, vertical columns, one just behind and somewhat under each eye, the muscles of which are embedded in the organ. Each organ is roughly oval in section and is composed of a number of parallel plates separated by electric connective tissue and made up of about 20 separate electroplaxes lying side by side. The number of plates in each organ does not exceed 200, but they are very thin and their constituent electroplaxes are deeply indented on the edges. The electroplax bends on itself so as to overlap on its own body at some points of considerable area, and so as to make it necessary for the overlapping portion to find room in the next layer in which to secure nerve and blood supply. From 3 to 5 of the larger electroplaxes form the central area of the layer and from 8 to 12 smaller ones are arranged around it and fill in the outline. The electroplax is placed in the organ with the electric layer upward and the nerve supply approaching it from above. The blood supply comes into contact with it on the lower or nutritive surface, which is evaginated into a number of papillæ that occupy more than two-thirds of the thickness of the electroplax. The nuclei of these papillæ are oval and differ slightly both in size and shape from those of the electric layer, which are evenly arranged in a series. The striation of this layer is remarkable and quite as definite and conspicuous as in the weakest of the Rajidæ (plate VI, fig. 3). It consists of fine, sharp lines spaced evenly and parallel to one another, but curved in many directions. In section one appears to be looking on various surfaces, the striations on one surface being parallel to each other but crossing above and below other sets of similar parallel striations. Dahlgren believes these lines to represent the edges of an equal number of curved and parallel surfaces, seen in actual or optical section. There is no variation in the distance between the lines, however, and no oblique or surface views of the striations appear (Dahlgren 36).

The nutritive layer is composed of two parts, one of which includes the nutritive nuclei, the evaginations, and the heaviest area of the striations. In the other layer there are no nuclei, but the striations continue and can be traced even into the thin electric layer, which contains a row of evenly spaced nuclei and the peculiar rods described by Dahlgren and in further detail by J. G. Hughes, of Professor Dahlgren's laboratory (62).

The nerve supply of *Astroscopus* consists of a number of medullated fibers that run between the layers in the electric tissue and end at all points on the electrical surface. The origin of the nerve supply, as well as the origin of the electric organs themselves, could not be surmised by Dahlgren and Silvester (36) at this time, owing to the complications in the adult. The muscles and nerves of the eye pass directly through the organs and the nerve which supplies the electric tissue is in some way curiously involved with the oculomotor nerve, but no connection

between the electric tissue and the eye-muscle tissue is evident, although the rectus inferior muscle has become so narrow as to appear as a mere thread and the rectus superior muscle is split into several parts by the passage of the electric nerve through it. The organ is bounded by the upper part of the muscle adductor mandibulæ, the muscle levator arcus palatini, and the anterior and posterior divisions of the muscle adductor arcus palatini.

The authors supposed the organs to have been derived from one of the bounding muscles, probably the muscle levator arcus palatini, since this has a more intimate connection with the organ than either of the other two, but the possibility was suggested of the tissue having arisen from the eye-muscles which pass through the organ. It was impossible to follow up either of these theories, however, without embryonic material, and a search for embryos was at once begun.



Astroscopus guttatus, 20 mm. embryo. Drawn from specimen by Bruce Horsfall.

*Opsanus* and *Porichthys* lay their eggs in nests or easily available places. This did not prove true of *Astroscopus*, however, and Professor Dahlgren studied the habits of the fish to find if possible where to look for the young forms. He found the habits of *Astroscopus* to be essentially similar to those of an allied form, *Uranoscopus scaber*, a native of the Bay of Naples. This fish, as explained by Dr. Cerruti (30), lays a pelagic egg which at once floats from the bottom, where it is deposited, to the surface, where it rapidly forms an embryo that lives on the surface for many weeks and months. *Astroscopus* has a large pelagic egg which is laid in May or June and develops into a larva very rapidly. It lives on the surface 50 to 60 miles from shore and gradually works inshore as it approaches adult life. Toward the latter part of the summer the young fish, over an inch in length, moves from the surface to the bottom and seeks the sand, in which it burrows and spends the greater part of its life. With this information extensive towing work was undertaken, and through the kindness of Dr. Henry B. Bigelow, of the Museum of Comparative Zoology at Harvard University, and of W. W. Welsh and Lewis Radcliffe, of the United States Bureau of Fisheries, the results of the

towings by the steamer *Fish Hawk* and the schooner *Grampus* were examined, and a few embryos of different sizes were found, from which the following results have been obtained. Recognition and thanks are also due to Dr. A. G. Mayer and his associates in the Carnegie Institution of Washington who have assisted in procuring these specimens.

In a few cases it was difficult to determine whether the embryos were *Astroscopus* larvæ or those of a nearly allied form, *Kathetostomata*, which lives in deep water off the Atlantic coast; but since the adult *Kathetostomata* has been studied and found to possess no electric organ, there remains no doubt that these embryos which possess the first rudiments of the electric organ are examples of *Astroscopus*. The embryos were all photographed before sectioning to aid in the identification of the species, but since *Astroscopus guttatus* and *Astroscopus y-græcum* have very similar electric organs in the adult, it matters very little for this work whether the embryos are all of one species or not. Most of them have been identified as *Astroscopus guttatus*.

## OBSERVATIONS.

The sectioned heads of these embryos have been handed over to me by Professor Dahlgren for the purpose of tracing the various steps in the development of this curious electric organ and to clear up such points concerning its innervation and blood supply as the material would allow. Some attention will also be given to the change in histological structures of the electric tissue during its development from the muscle tissues.

It quickly became evident that the electric tissue in the young embryos was being formed by the metamorphosing of certain parts of some of the eye-muscle, a phenomenon not hitherto met with and therefore of special interest.

### STUDY OF AN EMBRYO 9.5 MILLIMETERS IN LENGTH.

The head of this embryo was sectioned serially and transversely and reconstructed with 2 mm. wax at a magnification of 500 (plate 1). Some of the eye-muscles of this little embryo are already beginning to show a change, although no definite electric tissue has yet formed. The rectus externus, rectus internus, and rectus superior muscles show a definite darkened area on the side away from the eye-ball, which, upon examination, proves to be composed of cells smaller than the normal muscle-cells. Both the nuclei and the cytoplasm of these cells take the stain much more densely than the other cells, but this is the only sign of any modification of the cell structure (plate v, fig. 2).

Sections of a 4 mm. embryo were also studied with regard to this particular point, although the specimen was too poorly preserved for any more careful investigation. In this embryo areas corresponding

to those mentioned above were found on the same muscles and with the same topographical relation to the muscle-cells. They had the same dense stain, but were very much smaller in area, as indicated in figure 1 of plate v.

A few embryos of the species *Batrachus tau* were then sectioned in order to observe the muscle-tissues, as it was thought possible that the smaller and more numerous cells might represent the generating area of the muscle itself and have no connection with the electric tissue. In these embryos such areas were found on several of the muscles, but a very interesting point lay in the fact that in every case this area of generating tissue lay on the opposite side of the muscle from that on which the electric organs of *Astroscopus* are derived, *i. e.*, on the side toward the eye-ball. In *Astroscopus*, however, this area corresponds in every case with the position from which the electric organ is to be generated; moreover, no such areas could be found in *Astroscopus* on the muscles not forming electric tissue. For this reason I feel certain that the darkened areas represent the first beginnings of electric tissue. The possibility also arises that in the darkened areas on the muscles of the young *Batrachus* we may have a step in the evolution of the electric organs in the toad-fish group.

The innervation of the eye-muscle in the 9.5 mm. embryo is perfectly normal and no nerve-endings are seen even to approach the electric tissue. A résumé of the normal eye-muscles, their origin, insertion and innervation will here be given for reference (Herrick 61 and Wiedersheim 94). The eye-muscles are six in number—rectus internus, externus, inferior, and superior, and obliquus inferior and superior.

The rectus internus, externus, and superior originate in the subcranial canal at the extreme caudal end of the basioccipital. The rectus externus originates in the extreme caudal end of the canal and runs dorso-laterad to its insertion on the base of the eye-ball. It receives the entire abducent or sixth nerve.

The rectus internus originates near the caudal end of the canal in a groove on the dorsal side of the parasphenoid bone and runs along the inner sides of the orbits to its insertion on the cephalic border of the eye-ball. It receives a branch of the oculomotor nerve, or the third nerve.

The rectus superior originates in the cephalic end of the subcranial canal from the parasphenoid, under the rectus internus, and from the membranous roof of the canal over the same. It runs close to the rectus internus to the end of the canal, turns dorsal and laterad, and crosses the rectus inferior and optic nerve to reach its insertion. It receives a branch of the oculomotor nerve.

The rectus inferior arises from the basisphenoid bone and runs over the rectus internus, rectus superior, and optic nerve to its insertion. It receives a branch of the oculomotor.

The obliquus superior and inferior muscles arise far cephalad from the internasal cartilage and run caudal to their insertions.

The obliquus superior arises farther cephalad than the interior muscle and is inserted on the dorsal surface of the eye-ball. The obliquus inferior originates a little farther back from the dorsal wall of the cartilage and lies nearer the median line. It passes mediad from the superior muscle direct to the ventral side of the eye. The obliquus superior is innervated by the entire trochlear or fourth nerve and the obliquus inferior receives a branch of the oculomotor.

The sixth or abducent nerve arises from a center in the medulla some distance from the median line near the lateral surface of the brain. It passes through a foramen in the cranial wall into the dorso-lateral angle of the subcranial canal and passes direct to the lateral face of the rectus externus, which it enters.

The trochlear or fourth nerve arises from a separate center in the hind-brain just caudal to that of the third nerve. It leaves the brain behind the optic lobes and continues intracranially a short distance, when it pierces the cranial wall, turns dorsad, and moves direct to the dorsal side of the obliquus superior.

The oculomotor or third nerve is a large nerve arising in the mid-brain from the nucleus near the median line in part mesial of the large fasciculus longitudinalis dorsalis. There is no trace of the differentiation of the large electric motor-cells at this stage. The nerve leaves the brain and gives off its first branch to the obliquus inferior. Both branches pass at once through the cranial wall just mesial of the rectus externus. The branch to the obliquus inferior turns ventrad and passes the rectus externus, internus, and inferior on its way to the ventral face of the obliquus inferior. The main branch gives off another branch which divides and goes to the rectus internus and inferior, but the main branch itself divides again, both branches entering the rectus superior muscle, a point of significance in light of further investigations.

### STUDY OF AN EMBRYO 14 MILLIMETERS LONG.

The 14 mm. embryo was sectioned serially and transversely, but was too poorly preserved for very careful study. The region of the electric tissue on the three muscles, rectus externus, internus, and superior, is now much more clearly defined and has considerably increased, but no indication of electric tissue or any other muscle can be found. The electric cells have enlarged slightly and can be identified by their multinucleate state as well as by their dense-staining capacity. The electric area is now as large as the muscle area in width, though not in length (plate v, fig. 3). Nerve-fibers do not yet approach the electric tissue on any of the eye-muscles.

STUDY OF AN EMBRYO 20 MILLIMETERS IN LENGTH.

The head of the 20 mm. embryo was sectioned serially and transversely and reconstructed in 1 mm. wax at a magnification of 500. This embryo was so well preserved that a very careful study has been made of it (plates II and III).

The electric area has become definite electric tissue and is now seen for the first time on the obliquus superior muscle, making it evident that the electric tissue is generated from muscles which are innervated by the fourth and sixth nerves as well as from some which are innervated by the third nerve. The three rectus muscles which contribute to the electric tissue have a common origin in the subcranial canal, the rectus inferior muscle having a separate origin. The obliquus superior arises at some distance from the three rectus muscles, but is the more dorsal of the two obliquus muscles. The fourth and sixth nerves take no part in the innervation of the adult electric organs. The organs are exposed dorsally, on the other hand, and only those muscles which are nearest the dorsal surface of the head have contributed to their formation, the two inferior muscles on the ventral surface not being concerned. *Torpedo* is the only other fish known to have the electric organs on the exposed or the dorsal surface, even though it occupies all the space between the dorsal and ventral surfaces. This tendency to develop the electric organs on the exposed or dorsal surface may be compared with the opposite tendency of fishes and other animals to develop their luminous organs on the ventral or protected surface, as shown in *Porichthys*. This correlation of the protective organ with the exposed surface and the attractive organ with the protected surface may be the result of natural selection, even though Darwin (37) considered electric organs to be one of the greatest difficulties in the way of his theory.

The electric cells have assumed the form of electroplaxes (plate V, fig. 4). They have enlarged to about six times the diameter of the ordinary muscle-cells; and the large and numerous nuclei have rounded up close to the membrane, although a few remain scattered in the cytoplasm. The cytoplasm itself has become peculiarly vacuolated and very definite striations have appeared. In longitudinal section each electroplax shows the ventral end indented into long, finger-like processes (plate VI, fig. 1). The striations across these processes are continuous, as though the cell had been cut through at this point after the striations had been formed instead of the processes having grown out. The striations are perfectly definite and pass straight across the cell with no indication of the myofibrillation. Long, narrow vacuoles appear at intervals in the cytoplasm of the indented or evaginated end, while the dorsal end of the cytoplasm is filled with vacuoles of a smaller, rounder nature. This indentation is the beginning of the formation of the ventral papillæ of the adult electroplax.

Vacuoles are formed in cells when changes in surface tension occur such that the pressure inside the cell-wall is greater than that of the surrounding medium. The electroblasts are growing at an abnormal rate in the longitudinal direction and not at all in the other direction, so that the pressure inside the cell must be tremendous. If this tension reaches a certain point, the vacuoles may increase in size until they burst through the cell-wall. That this is happening in these electroblasts is shown by the long, narrow shape of the vacuoles at the ventral end, where many have already broken through to form the papillæ. This explains why the striations at this end appear to be broken across instead of being separate striations formed for each papilla. It also explains why in the adult electroplax many of the papillæ have connecting bridges of the same material as themselves (Dahlgren 36), for in such cases the vacuoles have merely persisted instead of breaking through. The tension at the ventral end far exceeds that of the dorsal end, for the small, round vacuoles finally disappear without breaking through the wall and the dorsal surface becomes straight and smooth, the dorsal cytoplasm homogeneous and unvacuolated.

The electric organ develops in four parts on each side of the eye, each of which is called an electric organ for convenience during its development. The rectus externus is the largest of the six eye-muscles and has a proportionately large electric organ. It is the first of the four to begin development. The central part of the tissue forms a broad band lying close to the muscle and curving from its dorsal to its ventral surface in a spiral. The ends of the tissue separate from the muscle ventrally, just caudad to the origin of the muscle, running caudad and ventrad, and dorsally, near the point of insertion, running craniad. This separation of the organs from the muscle with the turning and bending of the organs is accomplished by the elongation of the electroblasts at the point of separation. The growth of the cells, therefore, begins at either end of the organ and later progresses toward the center. Also, the electric organ of the rectus externus muscle, which was the first to begin development, is the first to begin to separate from the muscle-tissue (plates II and III, *R.* ex.).

The long, narrow electric organ of the rectus internus lies close to its surface and curves spirally from a point cranial and medial around the dorsal to the ventral side of the muscle. Dorsally the organ remains closely attached to the muscle, but ventrally it separates to run caudad a short distance. It is the second of the four electric organs to begin development and the second to begin to separate from the muscle (plates II and III, *R. int.*).

The electric organ of the rectus superior muscle lies close to the median side and does not curve around it nor separate from it. The obliquus superior is the last of the four muscles to develop an electric organ, which is correspondingly small, forming a short, broad band,

caudad and close to the muscle, about halfway between its origin and insertion (plates II and III, *R. su.*, *O. su.*). In the figures the electric area is stippled.

The number of electroblasts do not increase after once being formed. Each electroblast is the product of a single cell and each electroplax is the product of a single electroblast, so that the amount of electric tissue to be contributed by the various muscles has already been determined. It was most unfortunate that no embryo could be obtained representing a stage between that of the 20 mm. embryo and of the 33 mm. embryo, as it is between these two stages that the actual separation of the organs from the muscles takes place. The position of the electric organs in the 20 mm. stage, however, goes a long way toward explaining the real process, so that we are safe in drawing pretty definite conclusions without the intermediate stage.

Except that the nerves branch much more profusely in all of the muscles, no change has been noted in any but that branch of the oculomotor nerve which goes to the rectus superior. As noted above, the main branch of the oculomotor goes to the rectus superior in two divisions. The larger of these two divisions enters the muscle somewhat posterior to the smaller one, and is seen to have enlarged to nearly twice its original diameter. The small branch goes to all parts of the muscle, but the large one goes to the middle of the muscle, where it divides into many parts, all but one of which are seen to approach the electric organ of this muscle and stop. There is a considerable space between the muscle and the electric tissue, and the axones of the nerves must cross this space to enter the electric organ. Although the material was not favorably fixed for the study of nerves, a few fibers could be traced across the intervening space and into the electric organ. Unfortunately, the nerve-endings could not be seen in any of my material and I have had to pass over this point until more material can be obtained. The last division of this branch, which does not approach the electric organ, passes directly through the rectus superior muscle and can be traced ventrally and mesad until it approaches the electric organ of the rectus internus muscle. It was impossible to trace any of the fibers of this branch into the electric organ, but the nerve itself could be traced until it touched the electric tissue, so that there can be no doubt that the axones do pass in and that with better material they could be seen to be distributed among the electroplaxes of this organ as well as that of the rectus superior. This is the first indication that the nerve which innervates the rectus superior muscle is to innervate the electric organs also, but it is not yet clear that it is the only nerve which will do so, although it is clear that the electric organ of the rectus superior is not the only one to be innervated by it. Later it sends branches to all four of the electric organs.

A few electric motor-cells are found in the motor nucleus of the third nerve. It is of interest in this connection that the rectus superior muscle is neither the first of the muscles to develop electric tissue nor does it contribute the largest amount of tissue to the organs. On the other hand, it does not contribute the smallest amount either, so there is no apparent reason why the nerve of this particular muscle should be called on to do all the work. It might have been expected that the sixth nerve, which innervates the rectus externus muscle, would contribute to the electric organs, since that muscle has the largest of the four organs, or (on the other hand) that the trochlear or fourth nerve to the obliquus superior muscle would contribute, since that muscle has the smallest amount of electric tissue. As a matter of fact, subsequent study has shown that there are no electric motor-cells to be found anywhere in the brain except in the nucleus of the third nerve, no fibers from any other nerve or from any other branch of that nerve even approaching the electric tissue. When the third nerve emerges from the cranial wall the first of the muscles which it is to innervate which crosses its path is the rectus superior; it is also the first muscle which it enters. Whether this fact has any significance for the fact that this particular branch forms the electric nerve or not, I can not say, but no other explanation presents itself.

The circulation in the head of the 20 mm. embryo appears to be perfectly normal, presenting no points of difference from that of other non-electric toad-fishes. The external carotid artery runs craniad just dorsal to the rectus inferior muscle, and sends off small branches to the various eye-muscles on the way to the eye-ball; it then runs between the two oblique muscles and craniad below the eye-ball. The vessels to the eye-muscles send no branches to the electric organs, either before or after entering the muscles. The ophthalmic artery branches from the pseudobranch to run craniodorsad to the eye-ball, which it enters with one of the ciliary nerves from the fifth cranial. It gives off a small branch just dorsal to the obliquus inferior muscle, which anastomoses with the corresponding artery on the other side, but this branch has no connection with the electric organs.

### STUDY OF AN EMBRYO 33 MILLIMETERS IN LENGTH.

The head of the 33 mm. embryo was sectioned serially and transversely and reconstructed in 1 mm. wax at a magnification of 45. Four well-developed electric organs appear, completely separated from the eye-muscles (plate IV). They are quite separate from each other dorsally and ventrally, but in the center they are so closely folded together that at times only a thread of connective tissue separates them and without the previous studies it would be impossible to determine from which muscle the different organs have been generated, or in fact that they had been generated from muscle-tissue at all. It

can be seen, however, that the four organs are still distinct. Together they occupy the entire space between the eyes and the brain, and although they have been derived from only the dorsal muscles they extend almost as far in the ventral direction as in the dorsal, the only difference being that the ventral ends of the organs are narrower and more pointed than the dorsal ends (plate VII, fig. 2).

The electroplaxes have assumed an elongate shape, being in general from three to four times as long as they are broad. They still have quite a thick appearance, however, for while they have been growing rapidly in one direction they have not become any narrower in the other, the width of these electroplaxes being only slightly less than that of the original electroblast. They are arranged in parallel rows, but since all four of the organs slant in a different direction, the rows are not parallel to the surface of the embryo, and on the whole they are only fairly regularly arranged. Ventrally the surface is entirely cut up into papillæ and many vacuoles are seen in the process of forming more (plate VI, fig. 2). The dorsal area shows a decided change in structure. The surface has become flat and smooth, the indefinite area of the 20 mm. embryo having completely disappeared. A few scattered vacuoles persist, but they are very small and round. The three layers of the adult electroplax have now been formed: the ventral layer, which is nutritive in function, with scattered nutritive nuclei, many papillæ, vacuoles, and perfectly straight striations; the middle or intermediate layer, with no nuclei and no vacuoles, but with an abundance of striations; and the dorsal layer, with a few small, round vacuoles, a few pretty definite striations on its ventral edge, and a very regular series of oval electric nuclei. The rods described by Dahlgren and Hughes have not yet appeared.

In the previously described embryo some of the nuclei had rounded up close to the membrane, while others remained free in the cytoplasm, but no difference in the structure of the two kinds of nuclei could be noted (plate VI, fig. 1). It is now evident that those nuclei which were close to the edge of the membrane have become flattened to fit the space, so that they appear quite oval in shape, while the nuclei which remained in the cytoplasm have become the round nutritive nuclei. They are less numerous than the electric nuclei and are not regularly placed in a series, but scattered through the cytoplasm of the nutritive layer. The electric nuclei have each a single nucleolus from which the chromatin runs out in fine strands through the caryoplasm, whereas the nutritive nuclei have several aggregates of chromatin but no well-defined nucleolus.

The electric nerve is now well developed from the branch of the oculomotor which supplies the rectus superior muscle. It has assumed such large proportions that the rest of the third nerve has a diameter only one-fourth that of the electric nerve, and the third nerve itself is

three or four times as wide as either of the other nerves which supply the eye-muscles. The third and electric nerve leave the brain together from the same center, which is now filled with the large electric nuclei, occupying much more space than the ordinary third nucleus (plate VII, fig. 5). They appear mesial, dorsal, and ventral of the fasciculus longitudinalis dorsalis. The cells are large and egg-shaped, with very granular cytoplasm. A large nucleus lies at the broad pole of the cell-body. It is fairly round in shape and has a few strands of chromatin running through it, as well as a very small aggregate of chromatin which is fairly persistent. At the pole of this nucleus corresponding with the broad pole of the cell is a very definite round nucleolus with a vacuole on one side. This body takes the chromatin stain heavily, while the rest of the nucleus takes it very lightly and the cytoplasm of the cell with only medium density. In the adult the cells measure 32 by 56 microns at their broadest point.

The third nerve branches from the electric nerve immediately upon leaving the brain, but continues to run close to its side until it has passed through the cranial wall (plate VII, fig. 6). In speaking of the electric nerve, it will be understood that that branch of the third nerve which goes to the rectus superior is included and, for that matter, that the electric and third nerve are one from their origin, but are given separate names for convenience. The other branch will be known as the third nerve. After passing through the cranial wall they go direct to the rectus superior muscle. The third nerve then passes laterad around the muscle, dividing at the same time into three branches for the three muscles which it is to innervate (plate VII, fig. 4). The small ciliary nerve to the fifth cranial has up to this time been in such close connection with the third nerve as not to be distinguishable from it, but now separates and can be traced into the sclera of the eye. The three branches of the third nerve pass directly through the electric organs in their passage to the muscles, but otherwise their behavior is perfectly normal and as described for the 20 mm. embryo.

The electric nerve passes with its entire bulk into the rectus superior muscle, the branch which is to innervate the muscle itself being separated from it just previous to entering. The nerve is twice as wide as the muscle itself, so that it tears the tissue of the muscle apart as it enters, and when it divides in the muscle its branches separate the fibers until they lose all connection with each other. One very small branch of the electric nerve innervates the muscle; the rest pass out and go in all directions through the electric organs, dividing and redividing as they go until the branches are no wider than ordinary nerves. Some of the branches turn back dorsally, go around the organs, and enter from the dorsal end; others pass directly through the organs mesially and laterally and enter the organs from the ventral end, while still others push their way between the organs in a ventral direction,

entering the organs on either side as they go, so that no corner of the four electric organs escapes their reach, no matter how remote. It is possible to trace each nerve to the particular electroplax which it innervates, but since all are branches of the same nerve this would have no significance. The nerves enter the electric organs between the electroplaxes which they enter on the dorsal surface. They can be seen to reach all points on the surface, but the nerve-endings could not be observed because of the unsuitable fixation.

The fourth nerve can be seen to arise from its separate center in the brain and to have no connection with the electric nerves.

The circulation has made rapid advance since the 20 mm. stage. Although the blood-vessels in most instances differentiate more rapidly than nerves, the arteries to the electric organ are not formed until after the innervation has been completed. In the 33 mm. embryo the branches of the carotid which nourish the eye-muscles have begun to give off small vessels at intervals which enter from the ventral surface. A large branch is given off from the vessel which goes to the rectus superior and another from the vessel which goes to the rectus inferior; other smaller branches are contributed by the vessels which go to the other muscles. A point in this connection is the fact that those muscles which have no part either in the formation of the electric organ or in their innervation do contribute toward their nourishment, so that all of the six eye-muscles are in some way involved.

The rectus inferior muscle has become so reduced that its widest portion is no wider than the nerve which innervates it (plate I, *R. inf.*). It passes directly through the electric organs, but at its point of origin on the basiosphenoid bone there are no muscle-fibers at all, a thin connective-tissue tendon attaching it to the bone. At a point slightly dorsal and some distance posterior to its origin muscle-fibers begin to appear and the muscle grows gradually wider. It is small wonder that the eyes of *Astroscopus* do not have the power of movement of an ordinary fish when the rectus inferior muscle has degenerated to a mere tendon and the rectus superior has been split into several parts by the huge electric nerve.

### STUDY OF AN EMBRYO 45 MILLIMETERS LONG.

The head of the 45 mm. embryo was sectioned serially and transversely, but the changes showed so plainly that no reconstruction was made of it. It is now impossible to trace the divisions between the separate electric organs, there appearing one very large organ which occupies the entire space between the eye and the brain and extends from the dorsal surface to a point not far from the ventral surface of the embryo, completely inclosing the eye-muscle (plate VII, fig. 3 and figs. 5–10).

There is no change in either the innervation or the circulation of this embryo.

The electroplaxes have now become very narrow and elongate and are arranged in parallel rows, strictly parallel except at the extreme edges or where a muscle passes through. Ventrally the surface is completely broken up into papillæ by the vacuoles, a few of which still persist, forming bridges across from one to the other. The electric layer has completely lost its vacuoles, but no black rods can be seen. The striations of the nutritive layer have taken on an entirely new appearance, differing but little from those in the adult. They no longer pass straight across the cell, but are broken up into a large number of small, curving striations, running in all directions and over and under each other in a manner which gives the effect of a maze. They are divided into groups, however, each group being composed of a few very definite, sharp lines, strictly parallel to each other, but with no relation to the lines of any other group. The lines of one group are all in one curved plane. They may lie over or under another group, but not between the lines of another group. The optical effect of these lines is like that of normal muscle striations, there being a dark area close to a light area (plate VI, fig. 3, *adult*).

It can be seen in section that the curious infoldings and overlappings of electroplaxes are beginning to form. Some of the electroplaxes run along parallel to the rest for some distance and then drop down perpendicularly one, two, or three rows, when they turn and continue in a straight line between two other electroplaxes. The electroplaxes between which they pass come up close to them so as to fill in the spaces, but whether they have been cut in two by the dropping of the electroplax or whether it has merely passed between two shorter electroplaxes could not be determined. This peculiar phenomenon has not been described for the electric organs of any other fish, but a possible explanation for this lies in the fact that the electroplaxes of *Astroscopus* must turn as they grow in order to properly orient themselves with reference to each other and to the body-surface, so that it is not surprising to find that some of them have become twisted in this particular manner and remain so. In all the other electric fishes which have been studied up to the present time, with the exception of *Malopterurus*, the electric tissues have been derived from muscles which are so oriented from the start that the electroplaxes come off from them in the exact position best suited for their purpose. They have, therefore, only to increase in length and to multiply their nuclei in order to form the regular parallel rows which are invariably found in the adult organ.

It is not mere chance, however, that the electric organs are formed of parallel electroplaxes any more than it is by chance that the electroplaxes are long, narrow cells with a definite polarization. In order to get an electric current the cells must be parallel, they must be polarized,

and the current is more effective if they be long and narrow, since then the resistance to the current is less. In *Astroscopus* the electroplaxes are formed from four different muscles, running in four different directions. The necessity for orientation is therefore evident. The process takes place between the 20 mm. and the 45 mm. stages. In the 20 mm. embryo the electric tissue is still a part of the muscles, though separating from them at the ends. In the 33 mm. embryo the organs are quite separate from the eye-muscles, but still exist as four separate organs, each organ lying in the position in which it came off from the muscle, so that they lie in four different directions. The electroplaxes of each separate organ lie approximately equal to each other in the middle, but on the edges they may be found in all stages of orientation, some of them having assumed the shape of horse-shoes, crescents, etc.

From the first the electroplaxes are very evenly spaced in the longitudinal direction and closely interlocked in the other. The cells elongate as they turn and the two processes occurring at the same time probably account for the curious overlapping of the electroplaxes described above. There appears to be a much larger number of the short electroplaxes in the 33 mm. stage than there are of the longer electroplaxes of the 45 mm. stage—doubtless another expression of this peculiar turning which enables the microtome knife to cut them in various planes, so that there appears to be a larger number of them than there really is. This fact also lends grounds for the idea that the electroplaxes in dropping from one row to another may cut through an otherwise single electroplax, making two where there was but one.

The process of orientation has been practically completed by the 45 mm. stage when the electroplaxes are found in their final position, parallel to each other and to the body-surface. At the extreme edges the electroplaxes never do completely straighten out, for it would seem that the body is not wide enough to accommodate the rapid growth of the electroplaxes, which continue to grow as long as the growth of the fish continues. Another place where the electroplaxes do not become strictly parallel is where the muscles pass through the electric organ. There is always a considerable amount of space around the muscle and the electroplaxes bend in toward each other at the edges, making a wall around them. At the extreme dorsal and ventral surfaces of the organ, also, the electroplaxes are crowded up closer than usual. With these few exceptions, by the time the fish is 45 mm. long the arrangement of the electroplaxes is strictly parallel and at even distances from one another.

The extraordinary regularity of the spacing is a very striking point. The width of the area between the electroplaxes does not vary more than 0.5 micron anywhere in the organ. Looking to the other electric fishes for comparison, we find that, with the exception of *Malopterurus*, all exhibit this same remarkable regularity, but that in some forms the

electroplaxes are much wider apart than in others. For instance, in *Astroscopus* there is a distance of 12 microns between every two electroplaxes, while in the Rajidæ the distances vary in the different species from 15 to 75 microns. In *Torpedo occidentalis* there are 5 microns between the electroplaxes, in *Torpedo ocellata* 4 to 8, and in *Gymnotus* 15; while in the Mormyridæ the space is very large.

## EXPERIMENTAL.

It was hoped at one time that the shock of *Astroscopus* might be accurately measured and so given its place among the other electric fishes. One living specimen was sent from Norfolk, Virginia, to the Princeton aquarium, where, with the aid of a physicist, Professor Adams, of Princeton University, a few experiments were carried on. Unfortunately the specimen was so weak from exhaustion when it arrived that only fatigue phenomena could be observed, and since the specimen never revived it was impossible to measure the current with any accuracy. It was possible, however, to make a few observations of value. The direction of the current was tested and found to agree with Pacini's law (76)—in other words, to pass from the motor to the nutritive layer of the electroplax. With the exception of *Malopterurus*, all electric fishes examined in this regard have been found to agree with Pacini's law. The exception of *Malopterurus* in this respect is probably not a serious one, since it was already known to differ from other electric fishes in nearly all respects except the power to give electric shocks and in its possession of the characteristic transparent jelly-like areas.

In *Gymnotus* and *Mormyrus* (Garten 49), where the electric layer is posterior to the nutritive, the current passes from tail to head. In *Raja*, which has its electric area on the anterior side, the current passes from head to tail. In *Torpedo* the electric disk is on the ventral side and the current passes from ventral to dorsal, and now it is seen that in *Astroscopus* the current passes from dorsal to ventral, the electric surface being on the dorsal side. No living specimen of *Gymnarchus* has been obtained, but the general resemblance of the organs of this fish (both in structure and origin) to those of the other Mormyridæ leaves very little room for doubt that the current passes from tail to head, as in those fishes.

The current entering on the dorsal side in *Astroscopus* makes the dorsal surface negative to the ventral; the nerve-endings are therefore all on the negative side. Although the organs of the various fish are innervated in quite different ways, yet in every case the entire electric surface is covered with nerve-endings, so that if it be the nerve and not the organ which generates the electricity the amount of electric surface and the arrangement of the surfaces would still be significant.

## DISCUSSION.

Bernstein and Tschermak (13) have suggested that the electrical discharges may be produced by different concentrations of sodium chloride in the electroplaxes and in the intervening connective tissue, a theory which necessitates the presence of a membrane between the two solutions which is permeable to one kind of ions and not to the other. Such a membrane is not known to be present, but neither is there any evidence against its existence, and without it the bio-electric current would appear to be arising without the ionization of anything. The principle of the bio-electric current is that normal sodium chloride and concentrated sodium-chloride solutions coming in contact diffuse their ions at different rates, causing currents in small amounts, just as they do in a muscle where such a membrane is known to exist.

Engelmann (39) has compared the thin, dark areas (electric) of the electric organs with the isotropic portion of the muscle-tissue, and the thick, light area (nutritive) with the anisotropic portion. The action current of an electric organ is the same as that of an ordinary striated muscle, except that the arrangement of the electroplaxes in a column makes appreciable an otherwise insignificant current. The action current of muscle can only be detected by the galvanometer, while that of an electric organ can be felt by the hand. Muscle, however, can be stimulated to give off electricity by mechanical, thermal, and chemical means as well as by the stimulation of the nerve. It can also be effectively paralyzed by small doses of curare and atropin, so that the nerves themselves are not affected, whereas electric organs can not be paralyzed unless the nerves are rendered powerless.

The strength of the shock in fishes is made possible by the arrangement of the electroplaxes in a column. In a battery, when the cells are arranged so that all the positive poles are connected together and all the negative poles together, they are said to be arranged in parallel, and when each positive pole is connected with a negative one, they are said to be arranged in series. According to Ohm's law, $C=\frac{E}{R}$, where $C=$ the strength of the current measured in amperes, $E=$ the electromotive force measured in volts, and $R=$ the resistance measured in ohms. Now, when the cells are arranged in series the electromotive force of the combination is the sum of the electromotive forces of the several cells, and the resistance of the cells is the sum of the resistances of the separate cells, providing high voltage and therefore high shocking power, but little current. When the cells are arranged in parallel the electromotive force is the same as that of one cell, while the resistance is less, being inversely proportional to the number of cells, thus providing a large current but low shocking power. By combining these two arrangements—that is, by putting the cells of one group in series and then joining several such groups in parallel—various

degrees of shocking power with much or little current may be obtained (Kimball 67).

In the case of the electric fishes it would seem that the electric organ itself forms the battery in which the different concentrations of sodium chloride form the poles, and in which the electroplax takes the place of the battery cell; or if the organ be composed of columns, then each column is a complete battery in itself, in turn acting as a cell in the larger battery, the electric organ. The surrounding medium, salt or fresh as the case may be, forms the conductor, and the nerves form the key which closes the circuit. When the nerve is stimulated the circuit is closed and the organ gives a shock. The organ being self-excitatory, is peculiarly adapted to give interrupted shocks after the manner of an induction coil, for when the nerve has been restimulated by the first shock it will go on opening and closing the key until the organ is worn out by fatigue. Gotch has shown that it is as impossible to fatigue the electric tissue as it is to paralyze it unless the nerve be fatigued (50).

In nearly all the electric fishes the electric organs are divided into columns. In *Torpedo ocellata,* for example, there are 450 columns in each electric organ and 400 disks in each column (Gotch 50). The current in this fish goes from ventral to dorsal, the ventral surface being negative to the dorsal one. In each column the disk nearest the ventral surface of the body will present its negative side to the surface, while the disk nearest the dorsal end will present its positive side, so that to complete the circuit between these two points it will be necessary to connect a positive with a negative surface. Thus the electroplaxes of each column will be arranged in series, so that the voltage of a column will be equal to that of all 400 disks combined, the amperage that of one. The 450 columns of the electric organ, however, are arranged in parallel, since all the surfaces facing the dorsal side of the body will be positive and all those facing the ventral side will be negative. In *Torpedo ocellata,* therefore, the amperage will be 450 times that of one column, the voltage 400 times that of one electroplax, a condition providing for a large amount of electricity and at the same time for a comparatively strong shock. Salt water is a million times better conductor than fresh water (DuBois-Reymond), thus furnishing very little resistance, so that *Torpedo,* although a fish of sluggish habits, has everything in its favor for effectively shocking its enemies, high voltage, high amperage, and low resistance.

In *Gymnotus* there are four electric organs lying lengthwise in the body and divided into a variable number of columns, each of which may have as many as 10,000 electroplaxes. Here, as in *Torpedo,* the columns as well as the four organs themselves are arranged in parallel and the electroplaxes in series. The resistance of fresh water is very great, but the arrangement of the columns in parallel provides for a larger amount of electricity and the extraordinary number of electroplaxes in

series overcomes the resistance sufficiently to give a very strong shock. In *Malopterurus* also the arrangement of the disks is an extensive one, even though not apparently arranged in either parallel or series, and so is adapted to the high resistance of the water.

It has been calculated, (Schönlein 83) that the electromotive force in one disk of *Raja* is 0.03, in *Torpedo* 0.04, and in *Malopterurus* may reach as high as 0.45 volt. These results show that aside from the number of electroplaxes there is a specific difference in the power of the individual electroplax. It was most unfortunate that the voltage of *Astroscopus* could not be determined, as it might then be possible to explain why *Astroscopus*, which has as many as 200 electric layers in each organ, arranged in series, and with no apparent resistance, should still have a shock so much weaker than *Torpedo*, as all reports would indicate.

The organ of *Astroscopus*, unlike the other electric organs, is not divided into columns, the diameter of a single electric layer being equal to one-third the diameter of the fish. When a current passes through a copper wire the resistance to the passage of the current is inversely proportional to the diameter of the wire. Therefore, were the diameter of a single electric layer in *Astroscopus* equal to the sums of the diameters of the 450 columns in *Torpedo*, the amperage of *Astroscopus* would be equal to that of *Torpedo* with only one column. As a matter of fact, the diameter of the organ in *Astroscopus* is much less than that of the columns in *Torpedo*, although the exact amount has not been computed. The amperage is therefore low, but the voltage being the sum of the 200 electric layers should be a little less than half that of *Torpedo ocellata*. Since it is known to be less than that, it must be that the qualitative differences in the structure of the electroplaxes themselves may offer various grades of resistance and so account for otherwise inexplicable differences in voltage. Still, the organ of *Astroscopus* has been measured only in small and much fatigued fishes.

A comparison of the marine electric fishes demonstrates that with the increase in voltage there is correlated not only an increase in the number of columns and in the electroplaxes in a column, but also a decrease in the width of the electroplaxes and in the area between them. In the fresh-water fishes the same general principles hold, except that in *Gymnotus* the electroplaxes are only slightly thinner than in the Mormyridæ. The thickness in *Mormyrus* is 450 microns, in the Rajidæ from 300 to 700, and in *Gymnotus* 200, in contrast to 35 in *Astroscopus* and 15 in *Torpedo*. In comparison with the number of the electroplaxes in a column, however, the electroplax in *Gymnotus* is not a great deal thicker than that of *Torpedo*, so it is possible that the amount of material may affect the strength of the shock by offering some resistance to the current.

It has been noted that in the so-called weak electric fishes the nutritive layer of the electroplax is very definitely striated, as though it had

not lost all relation to the original muscle-cell. Also, in the Mormyridæ the electric organs of some of the forms are connected to the muscle in the adult instead of being completely free as usual. In *Astroscopus* the striations are as definite as in the weakest fishes and so numerous as to be seen up into the electric layer. In *Torpedo* and *Gymnotus*, on the other hand, the electroplaxes have no structures to remind one of their muscular origin. In *Torpedo* they exist in the embryo only and are mere fibrillations, which in the case of *Gymnotus* are so reduced as to be recognized as striations only from a comparative study of the other forms. Are we here witnessing one phase in the evolution of electric organs, and are we justified in making these comparisons between such widely unrelated forms? We can not, of course, consider the transition from a mormyrid to one of the Rajidæ a case of natural selection, but if selection is taking place separately in each of the groups we may say that in the Mormyridæ the evolution of the electric organs has advanced to a much less degree than in *Torpedo* or in *Gymnotus*, and the lack of transitional stages in the groups themselves may not mean that they do not or have not existed. In the Rajidæ a very definite series exists, from forms with wholly undifferentiated electric tissue to those with definite electroplaxes, and not all torpedoes have shocks of the same intensity. It is probable, therefore, that the appearance of electric organs in the separate groups is a case of parallelism, evolution having taken place independently in each individual group. This parallelism may be accounted for by assuming that the evolutionary processes are continually working on the minute electrical discharge known to accompany the activities of muscle-cells, and that under proper environmental stimulus any fish might develop similar organs. What external factors initiate this development are not apparent, since electric organs appear to have developed simultaneously in fishes which lie buried in the sand on the bottom of the ocean and in fishes which swim freely about in both fresh and salt waters. The position of the organ in the body of the fish is individually adapted to the mode of life, those fishes which are commonly attacked from above developing electric organs in a dorso-ventral position, while those which swim freely in the water have antero-posterior electric organs. The primary use of the organ is probably that of protection, the capturing of food being a secondary adaptation.

## SUMMARY.

1. Each of the two electric organs of *Astroscopus guttatus* is originally composed of four separate elements, each derived from one of the six eye-muscles. The rectus inferior and obliquus inferior muscles are the nearest to the ventral surfaces of the animal and are the only ones which do not contribute any electric tissue to the formation of the organ.

2. The four organs begin to differentiate before the embryo is 14 mm. in length. The first indication of the change is a slight darkening of the muscle-cells on one edge of the muscle, followed by a multiplication of nuclei and the rapid growth of the cells. No such areas form on muscles which do not form electric organs.

3. The electroblasts are completely differentiated by the 20 mm. stage and the organs have separated from the muscle by the 35 mm. stage.

4. Between the 33 mm. and the 45 mm. stages the four organs, now separated from the eye-muscle, orient themselves until their constituent electroplaxes become parallel to the dorsal and ventral surfaces of the body of the fish and unite to form one large organ with a diameter equal to one-third the diameter of the head of the fish.

5. Each electroplax is formed by the modification of a single myoblast cell.

6. The nuclei multiply and differentiate to form electric and motor nuclei. The electric nuclei are wide and flat, and arranged in a regular series on the negative surface of the electroplax. They have a definite nucleolus and faint chromatic threads. The nutritive nuclei are large and round, with several aggregates of chromatin but no definite nucleolus.

7. The cytoplasm differentiates into electric and nutritive layers.

8. There are no easily visible myofibrillations, but the longitudinal striations persist in the nutritive layer and are broken up into short, curved striations, very definite in outline. They can be traced into the electric layer.

9. The vacuoles of the dorsal surface disappear, but those of the ventral surface break through the membrane to form the papillæ and the protoplasmic bridges which characterize the nutritive surface.

10. The electroplax is 35 microns in width, one-third of which is electric and two-thirds nutritive material. It is twice as wide as the electroplax of *Torpedo*, but only half as wide as that of the weak electric fishes.

11. The electroplaxes are arranged in a parallel series, but some are carried down one or more layers in the process of orientation, so that they form a part of the lower layers.

12. The electric organ is innervated by that branch of the oculomotor nerve which supplies the rectus superior muscle. It begins to differentiate during the 20 mm. stage and is complete by the 33 mm. stage.

13. The electric and third nerves leave the brain together from the same nucleus, but separate before passing through the cranial wall. The electric nerve passes bodily into the rectus superior muscle, the fibers of which are torn apart by the process.

14. The branches of the nerve reach every corner of the electric organ and end on the dorsal surface of each electroplax.

15. The electric motor-cells are formed in the region of the third nucleus, mesial, dorsal, and ventral, of the fasciculus longitudinalis dorsalis. They are large, egg-shaped cells with prominent nucleus and nucleolus.

16. The blood supply of the electric organ is furnished by vessels from those branches of the external carotid artery which go to the six eye-muscles.

17. The blood supply does not begin to differentiate until the embryo is nearly 33 mm. long, and is not complete until the 45 mm. stage. It is the last of the structures connected with the electric organs to begin development.

18. The electric organ of *Astroscopus* can be stimulated by touch, and by chemical or electrical stimuli applied to the skin. It is also probably operated from some of the optic centers.

19. The current passes from the dorsal to the ventral surface in accordance with Pacini's law.

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## EXPLANATION OF PLATES.

I. 9.5 mm. embryo, ×250. Diagrammatic anterior view of eyes to show relation of electric tissue (stippled) to eye-muscles.

R. Ex.....Rectus externus muscle.
R. Int.....Rectus internus muscle.
R. Inf.....Rectus inferior muscle.
R. Sup.....Rectus superior muscle.
O. Inf.....Obliquus inferior muscle.
O. Sup.....Obliquus superior muscle.
Ex. C.....External carotid artery.

II. 20 mm. embryo, ×200. Diagrammatic anterior view of eyes to show increase of electric tissue (stippled) and relation of cranial nerves to eye-muscles. Roman numerals indicate cranial nerves.

III. 20 mm. embryo, ×475. Diagrammatic median view of left eye.

IV. 33 mm. embryo, ×200. Diagrammatic anterior view of eyes to show relation of nerve III to eye-muscles and to the four separate electric organs (stippled). To left is shown the electric branch of nerve III and to right the oculomotor branch.

V. Rectus internus muscle. Four stages to show gradual growth and differentiation of electric tissue on the young muscle.

Fig. 1. 4 mm. embryo. Cross-section. Electric area slightly darker than muscle area.

Fig. 2. 9.5 mm. embryo. Cross-section. Electric area increased in size and staining capacity.

Fig. 3. 14 mm. embryo. Oblique section. Electroblasts multinucleate.

Fig. 4. 20 mm. embryo. Cross-section showing only a portion of the electric area. Electroblasts vacuolated. Myoblasts striated.

El.....Electroblast, multinucleate.
M.....Myoblast.
V.....Vacuole.
Un. N.....Undifferentiated nucleus of electroblast
N.....Nucleus of myoblast.
S.....Striations.

VI. Electroplaxes. Three stages to show growth and differentiation of adult electroplax from single electroblast.

Fig. 1. 20 mm. embryo. Single electroblast. Longitudinal section to show formation of ventral papillæ from vacuoles. Nuclei undifferentiated.

El.....Electric area of electroblast.
N.....Nutritive area.
D. V.....Dorsal vacuole.
V. V.....Ventral vacuole.
Un Nu.....Undifferentiated nucleus.
S.....Striation.
P.....Papilla.

Fig. 2. 33 mm. embryo. Longitudinal section of electroplax. Nutritive and electric areas differentiated. Striations straight and regular.

El. Nu.....Electric nucleus.
N. Nu.....Nutritive nucleus.

VI. Electroplaxes.—*Continued.*

Fig. 3. Adult. Longitudinal section of portion of electroplax. Dorsal vacuoles have entirely disappeared. Striations broken and curved.

Ch. R.....Chromatic rod.
Ne.....Nerve-fiber.
B.....Blood-vessel.
C.....Connective tissue.
C. V.....Vacuole in connective tissue.

VII. Photomicrographs.

Fig. 1. 20 mm. embryo, ×80. Electric area to show relation of electric to muscle tissue.

R. Ex.....Rectus externus muscle.
R. Su.....Rectus superior muscle.
R. Inf.....Rectus inferior muscle
A.....Artery.

Fig. 2. 33 mm. embryo, ×35. Electric area to show four separate electric organs in position.

Fig. 3. 80 mm. embryo, ×35. Portion of electric area. Fibers of rectus superior muscle separated by electric nerve. Overlapping of electroplaxes shown.

Fig. 4. 33 mm. embryo, ×85. Electric nerve passing through rectus superior muscle. Oculomotor nerve. Three branches of oculomotor to right.

Fig. 5. 45 mm. embryo, ×85. Electric and oculomotor branches of III nerve, immediately after leaving brain. Ganglion of V nerve below.

Fig. 6. 45 mm. embryo, ×85. Electric and oculomotor branches of III nerve passing through the foramen in the cranial wall.

Fig. 7. 45 mm. embryo, ×85. Electric nerve in rectus superior muscle. Branches of oculomotor to right of muscle.

Fig. 8. 45 mm. embryo, ×85. Large branch of electric nerve entering electric organ. Oculomotor to right.

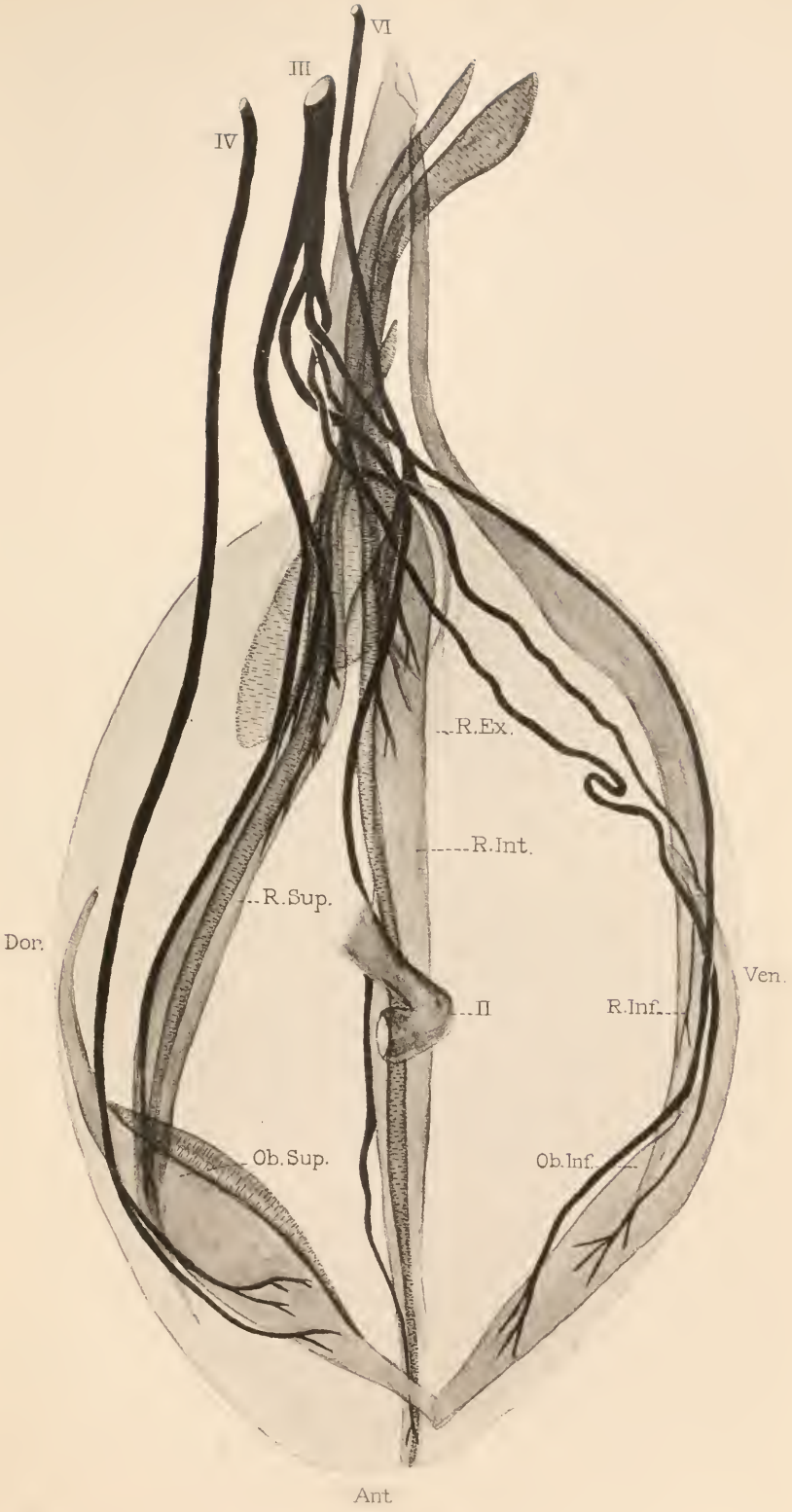
Fig. 9. 45 mm. embryo, ×85. View from opposite side of embryo. Fibers of rectus superior muscle entirely separated by electric nerve. Nerve breaking up in muscle to form branches. Oculomotor to left.

Fig. 10. 45 mm. embryo, ×85. Branches of electric nerve after leaving rectus superior muscle, going to various parts of the electric organ. Branches of oculomotor separating to go to muscles.

Fig. 11. 80 mm. embryo, ×85. Fibers of rectus superior muscle almost obliterated by the electric nerve.

R. Ex.
R. Su.
R. Inf.
II
Ex. C.
R. Int.
Ob. Inf.
Ob. Su.

VI
IV
III
Ex.
II
R.Int
Ob.Inf.
Ob.Sup.
R.Sup.
R.Inf.
R.Ex.
Left
Right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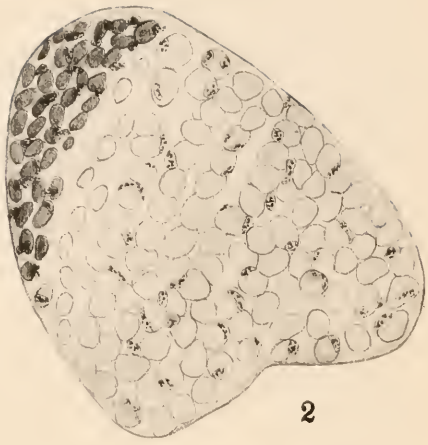

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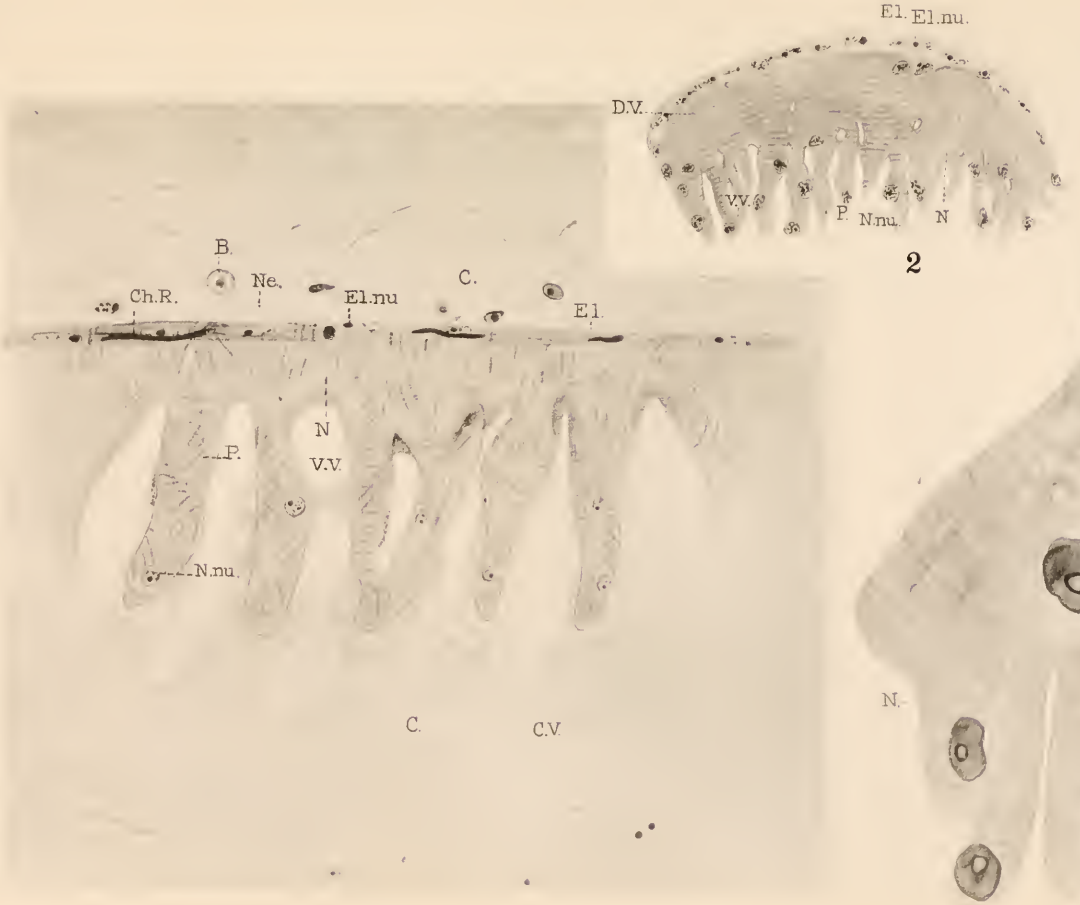
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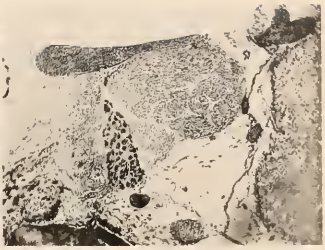

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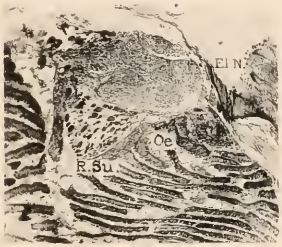


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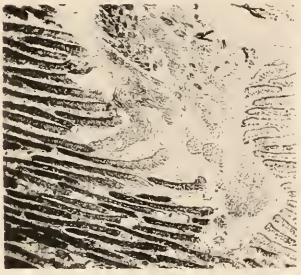

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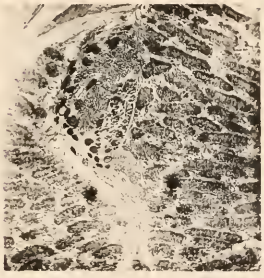

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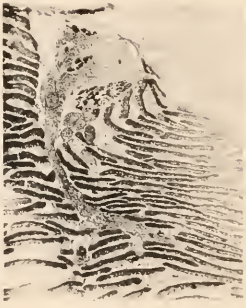

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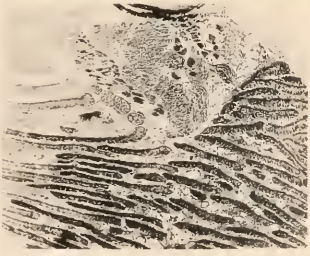

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# VII.

# TOXIC EFFECTS DUE TO HIGH TEMPERATURE.

By ALFRED GOLDSBOROUGH MAYER.

# TOXIC EFFECTS DUE TO HIGH TEMPERATURE.

By Alfred Goldsborough Mayer.

The experiments cited below appear to indicate that death from high temperature may be due to the accumulation of acid in the tissues.

Reef corals from Tortugas, Florida, were kept at a constant temperature in warm ocean-water for 60 minutes in a thermostat, in the dark the temperature remaining constant within about 0.1° C. throughout the hour. In this manner the temperature was found that is just sufficient to kill the coral. The results are as follows:

| | °C. | | °C. |
|---|---|---|---|
| Acropora muricata ..... | 34.7 | Mæandra areolata..... | 36.8 |
| Orbicella annularis..... | 35.6 | Porites furcata..... | 36.85 |
| Porites astræoides..... | 35.8 | Favia fragum..... | 37.05 |
| Porites clavaria..... | 36.4 | Siderastrea radians..... | 38.2 |

It is apparent that those corals which live in cool, relatively agitated water, free from silt, are those that can not withstand high temperatures, whereas those which live in the hot, silt-laden shallows near shore are, generally speaking, forms which can resist high temperature. *Favia fragum* is, however, an exception, for it lives not only in the shallows close to shore, but also in the pure water of the seaward reefs.

If sea-water be charged to saturation with carbon-dioxide gas from a soda-water siphon, the corals show nearly the same relative resistance to the toxic effect of carbonic acid as they do to high temperature. Thus these corals from least to most resistant are *Acropora muricata*, *Orbicella annularis*, *Porites astræoides*, *P. clavaria*, *P. furcata*, *Mæandra areolata*, *Favia fragum*, *Siderastrea radians*. *A. muricata* die in less than an hour and *S. radians* survive for more than 4 hours. In my experiments, however, *M. areolata* appeared to be slightly more resistant to $CO_2$ than does *Porites furcata*, whereas the reverse is the case with high temperature; but the two forms are so nearly alike in their reaction that the discrepancy may be due to errors in experimentation or to individual differences of constitution in the specimens, for there is considerable range in this respect. The toxic effect of $CO_2$ may, however, be independent of asphyxiation, and this supposition is strengthened by the fact that with the exception of *Acropora muricata*, all of these corals can survive in the dark for more than 11 hours in sea-water deprived of oxygen under an air-pump; and even *Acropora muricata* can withstand 6 hours of this treatment.

It will be recalled that Henze (1910) found that sea-anemones consume less oxygen as the oxygen in the surrounding sea-water is reduced; and in 1917 McClendon discovered that the medusa *Cassiopea* can live

in the dark for more than 7 hours without oxygen and under this condition it produces no appreciable amount of $CO_2$. In other words, these cœlenterates can, if deprived of oxygen, suspend their metabolism for a more or less protracted period without apparent injury.

Moreover, I find that a constant high temperature causes death in the same time, whether the sea-water surrounding the corals has the normal concentration of about 4.3 c.c. oxygen per liter, or the oxygen be supersaturated at 6.6 c.c. per liter, or reduced by being placed under an air-pump to 1.7 c.c. per liter. Apparently, therefore, there is no direct relation between the oxygen supply and the death temperature. The death temperature also remains the same whether the corals be in sunlight or in darkness.

Using Winkler's method, tests were made upon five of the common reef corals of Tortugas to determine their relative rates of consumption of oxygen. In these experiments the corals were kept in the dark to prevent photosynthesis in their commensal plant-cells, for in sunlight the surrounding water soon becomes supersaturated with oxygen from this cause. Care was also taken to use very small specimens of the various species of corals and to place them in large glass jars hermetically sealed, each containing about 2 liters of sea-water. The corals were kept for 5 hours in these jars in darkness in a water thermostat at 28.5° C. and daily experiments were made upon each of them for 11 successive days. The polyp-bearing area of each coral was then determined by a planimeter and the relative weight of living substance per square centimeter was obtained by killing specimens of these corals in formalin, hardening in alcohol, and then dissolving away the calcareous substance in nitric acid and weighing the tissue in sea-water. Prepared in this manner a square centimeter of the animal substance of *Acropora muricata* weighs 0.032 gram; while *Orbicella annularis* weighs 0.17, *Favia fragum* 0.059, *Mœandra areolata* 0.109, and *Siderastrea radians* 0.125 gram per square centimeter.

The experiments showed that *Siderastrea radians* at 28.5° C. consumes 0.0032 c.c. of oxygen per square centimeter of its polyp-bearing surface per hour, and as each square centimeter of the fleshy substance of *S. radians* weighs 0.125 gram, each gram of animal matter of the coral consumes 0.0256 c.c. of oxygen per hour, the oxygen being measured at 760 mm. pressure and 0° C. Thus taking the behavior of *S. radians* as a standard and calling its oxygen consumption per gram of its living substance 1, the relative rates of oxygen consumption per hour in the other corals at 28.5° C. per gram of living substance of the coral are as shown in the table herewith.

| Name of coral. | Relative oxygen consumption. |
|---|---|
| Siderastrea radians. | 1.0 |
| Mœandra areolata.. | 3.8 |
| Favia fragum..... | 5.5 |
| Orbicella annularis. | 6.1 |
| Acropora muricata. | 18.7 |

If the rate of consumption of oxygen be taken as a measure of the metabolism of the corals, it appears that the metabolic activity bears an inverse ratio to the coral's ability to withstand the effects of carbonic acid and their ability to resist high temperature follows nearly the same law. It seems possible, therefore, that under the influence of high temperature carbonic acid may accumulate in the tissues faster than it can be eliminated, and acids being toxic would soon cause death.

In the case of the scyphomedusa *Cassiopea*, I find that for temperatures below 37° there is no time factor—that is to say, if the pulsating subumbrella ring deprived of sense-organs and having an entrapped neurogenic contraction wave be taken from sea-water of about 29° and placed in water of 36° C., it at once assumes a rate characteristic of this higher temperature, and this rate is the same as if the temperature had been slowly raised so that two or more hours elapsed before the temperature rose from 29° to 36° C. Moreover, the reaction is completely reversible, the rate returning at once to the original when the ring is replaced in sea-water at 29°. At about 37° or 38°, however, the rate of the nerve impulse begins to decline sharply, and I find that this is subject to a time factor, the decline becoming more and more pronounced as the heat, even though constant in temperature, is continued. Moreover, when the superheated ring is replaced in sea-water at 29° C., the pulsation is slower than it was before being subjected to the excessive heat. A time factor for the effect of extreme heat has been known since the time of Sachs (1865) and has been studied by Blackman (1905) and others. After about an hour, more or less complete recovery of rate may take place, especially if the heat had not been too great or exposure to its influences too long. In other words, at injuriously high temperatures $CO_2$ may accumulate more rapidly than the tissues can eliminate it and the time-factor, according to my hypothesis, is due to this fact.

Thus in a typical case, a nerve-wave in *Cassiopea* having a rate of 100 at 29.3° had the following rates when heated to 37.8° C.: 100 at 29.3°, 125 at 35.6°, 126 at 36.7°, 127 at 37.3°, 120 at 37.8°. Thus the nerve-conduction became more and more rapid up to 37.3° C., above which it declined sharply, becoming 120 after being for about 20 minutes at 37.8° C. The animal was then taken from 37.8° C. and replaced in sea-water at 29.3° C., and its rate declined at once to 80, thus being 20 per cent less rapid than it was at the beginning of the experiment; but after remaining in sea-water at 29.3° C. for nearly 2 hours the original rate was completely restored.

It will be recalled that Blackman (1905) and Harvey (1911) advanced the theory that some enzyme might be destroyed by the excessive heat, and, being essential to nerve-conduction, its loss caused the rate to decline. It is also possible, however, that some toxic-acid

substance is formed under the influence of excessive heat, its rate of formation being commensurate with the metabolism of the tissues. It is easy to see how an acid of this sort might be eliminated and the rate gradually restored when the animal is replaced in normal sea-water, whereas if an enzyme were destroyed it might not so readily be replaced.

In any event, one or the other of the above-mentioned hypotheses seems more in accord with the facts than does Winterstein's asphyxiation theory, or the theory that death from heat is due to coagulation of proteid substances. Death occurs at too low a temperature for coagulation in most if not all proteids; and when killed the animals are fully relaxed, as shown by Harvey. Also, coagulated proteins could not readily be eliminated when the animal was restored to water at normal temperature, coagulation being a practically non-reversible process.

## SUMMARY.

It seems possible that death from high temperature may be due to the accumulation of acid (possibly $H_2CO_3$) in the tissues, the rate of formation of this acid being related to the rate of metabolism of the tissues. Thus animals of the same class having a high rate of metabolism, as measured by oxygen consumption, are more sensitive to heat and to $CO_2$ than are those having a low rate of metabolism.

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# VIII.

# NERVE-CONDUCTION IN DILUTED AND IN CONCENTRATED SEA-WATER

By ALFRED GOLDSBOROUGH MAYER.

One text-figure.

# NERVE-CONDUCTION IN DILUTED AND IN CONCENTRATED SEA-WATER.

By Alfred Goldsborough Mayer.

Ring-shaped strips of subumbrella tissue of the scyphomedusa *Cassiopea xamachana* were deprived of marginal sense-organs and placed in concentrated sea-water in order to determine the effect of concentration of electrolytes upon their rate of nerve-conduction.

These results, combined with those previously obtained[1] with diluted sea-water, are as follows:

Table I.

(Illustrated by figure 1.)

| Salinity 0/00 salt in grams in 1,000 grams of sea-water. | Relative salinity, that of normal sea-water being 100. | $x$ Relative electrical conductivity at 30° C., that of normal sea-water being 100. | Hydrogen-ion concentration of the solution in terms of $P_H$. | $y$ Relative rate of nerve-conduction, that in normal sea-water being 100. | Probable error of rate. | Remarks. |
|---|---|---|---|---|---|---|
| 18.13 | 0.5 | 54.1 | 8.1 | 54.16 | 0.79 | Normal sea-water of 8.23 $P_H$ diluted with distilled water of 7.9 $P_H$. |
| 21.74 | 0.6 | 64.3 | 8.2 | 65.72 | 1.01 | |
| 25.37 | 0.7 | 71 5 | 8.2 | 73.91 | 1.16 | |
| 29.00 | 0.8 | 81.4 | 8.2 | 79.51 | 1.18 | |
| 32.61 | 0.9 | 92.2 | 8.2 | 91.44 | 1.00 | |
| 34.43 | 0.95 | 96.4 | 8.2 | 96.23 | 0.67 | |
| 36.24 | 1.00 | 100 | 8.22 | 100. | .... | Normal sea-water. |
| 39.58 | 1.092 | 107.8 | 8.23 | 101.3 | 0.52 | Sea-water evaporated in sunlight, and its alkalinity restored to 8.1 to 8.2 $P_H$ with HCl. |
| 41.59 | 1.148 | 113.6 | 8.2 | 107.5 | 0.71 | |
| 49.18 | 1.357 | 128.7 | 8.13 | 104.3 | 0.95 | |
| 60.96 | 1.682 | 153.9 | 8.1 | 76.9 | 0.63 | |

The sea-water was concentrated by evaporation in sunlight, and its alkalinity reduced to that of normal sea-water by adding a slight amount of hydrochloric acid, the hydrogen-ion concentration being determined colorimetrically by comparison with a graded set of thymol-sulphonephthalein tubes prepared and standardized by Professor J. F. McClendon. These readings were also checked by comparison with those of a Leeds and Northrup potentiometer.

The hydrogen-ion concentration of the sea-water at Tortugas is usually between 8.1 and 8.23 $P_H$, and many experiments made in 1917 showed that the rate of nerve-conduction remains practically constant

[1]Mayer, A. G., 1917, Papers from Department of Marine Biology, Carnegie Inst. Wash., vol. 11, pp. 1–20.

and normal in sea-waters ranging from 7 to 8.65 $P_H$; the relatively acid water is made from normal sea-water treated with HCl and the alkaline water from normal sea-water treated with $HNaCO_3$, and $Na_2CO_3$.

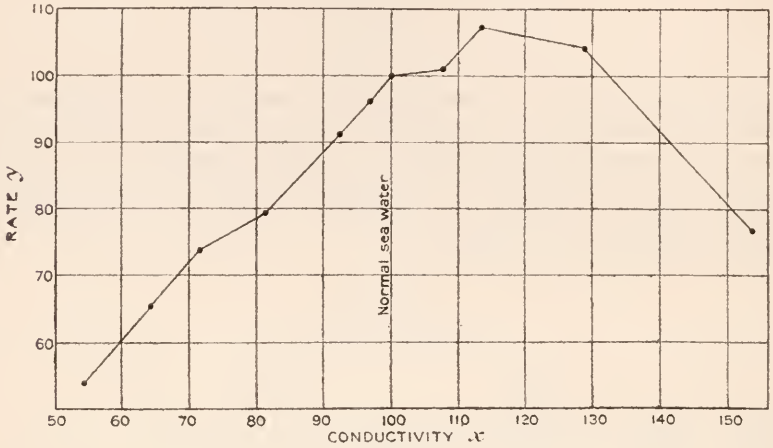


FIGURE 1.

If, however, the water is made as acid as 6.7 $P_H$, the rate falls slightly so as to be about 98, that in normal sea-water being 100; and at 6.3 $P_H$ the rate declines to 80 with greatly reduced muscular activity; but it recovers in all respects almost immediately upon being replaced in normal sea-water.

At 30° C. the neutral point is about 6.8 $P_H$ and it then appears that in sea-water any excess of $H^{\cdot}$ over $OH'$ is decidedly depressant, while correspondingly alkaline sea-water produces no ill effects.

Assuming the electrical conductivity of normal sea-water of 36.24 0/00 salinity and 8.22 $P_H$ to be 100, it appears from table I and figure 1 that the rate of nerve-conduction augments in practically a straight line as the relative electrical conductivity of the sea-water increases from 51 to about 108, above which the rate falls off rapidly, becoming about 77 in concentrated sea-water having an electrical conductivity of 152.9.

The formula is $y = 0.945x + 4.4$; $y$ is the rate of nerve-conduction, that in natural sea-water being 100; $x$ is the electrical conductivity of the sea-water, that of normal sea-water being 100.

The electrical conductivity of the sea-water was determined by Kohlrausch's method, using a tunable telephone and a Leeds and Northrup revolving drum bridge. The figures given in table I are for sea-water at 30° C.

It was found that the electrical conductivity of sea-water of 36.24 0/00 salinity and 8.22 $P_H$, at 30° C. was 4.21 times that of N/10 KCl at the same temperature. If, however, the sea-water be compared

with this potassium-chloride solution, both at 25° C., the ratio of their electrical conductivities became as 1 to 4.179.

The salinity of the sea-water was determined by titration with silver nitrate, using potassium chromate as an indicator and titrating against a sample of standard sea-water from Professor Knŭdsen's laboratory.

The fact that the rate of nerve-conduction increases in a straight-line ratio in comparison with the increase of electrical conductivity suggests a causal relation between the two, as was pointed out by Ralph S. Lillie, 1916,[1] but the same ratio exists between the concentration of the dissociated cations $Na^{\cdot}$, $Ca^{\cdot\cdot}$, $Mg^{\cdot\cdot}$, and $K^{\cdot}$, surrounding the nerves and the rate of nerve-conduction; and thus the rate may be dependent upon the concentration of these electrolytes rather than upon their electrical conductivity as such. Thus, in experiments made in 1917 upon *Cassiopea*, we find that if the electrical conductivity of 0.601 *m.* NaCl be taken as 1.00, that of an isotonic solution composed of 81.1 c.c. of 0.601 *m.* NaCl + 14.36 of 0.39 *m.* $MgCl_2$ is 0.932; yet if the rate in the pure sodium chloride be 100, that in the NaCl+$MgCl_2$ is 115. Thus the rate has increased while the electrical conductivity has diminished. This experiment is a striking illustration of Loeb's law that a bivalent cation tends to offset the injurious effects of a univalent cation and even magnesium, a well-known depressant, acts as a stimulant for rate of nerve-conduction in association with sodium.

Comparing the effects of these solutions with that of normal sea-water, all being practically isotonic one with the other, we find:

Rate of nerve-conduction is 100 in natural sea-water of 36.24 0/00 salinity, 8.22 $P_H$, and 1.00 relative electrical conductivity.

Rate of nerve-conduction is 79.6 in 0.601 *m.* NaCl of 8.2 $P_H$, and 0.996 relative electrical conductivity.

Rate of nerve-conduction is 92.2 in 81.1 c.c. of 0.601 *m.* NaCl+ 14.36 of 0.39 *m.* $MgCl_2$ of 8.2 $P_H$, and 0.94 relative electrical conductivity.

It may be of interest to see that diluted sea-water is less depressant for nerve-conduction than abnormally concentrated sea-water.

The injurious effects of concentrated sea-water upon regeneration and growth have been studied by Loeb[2] and by Goldfarb,[3] and there is a general resemblance between their curves and ours for the rate of nerve-conduction, excepting that for regeneration somewhat dilute sea-water seems to be more favorable than normal sea-water, whereas in nerve-conduction the highest rate is obtained in slightly concentrated sea-water.

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[1]Lillie, R. S., 1916, American Journal Physiology, vol. 41, pp. 126–136.

[2]Loeb, J., 1891, Organbildung und Wachsthum, 82 pp., Würzburg.

[3]Goldfarb, A. J., 1914, Papers from the Tortugas Laboratory, Carnegie Inst. Wash. Pub. No. 183, pp. 83–94.

# IX.

# A STUDY OF RESPIRATION IN ALCYONARIA.

BY LEWIS R. CARY,

Department of Biology, Princeton University.

# A STUDY OF RESPIRATION IN ALCYONARIA.

By Lewis R. Cary.

Although the respiration of many species of invertebrates has been studied in considerable detail, the only references to that of Alcyonaria which have come to the attention of the writer are those given by Montuori (1913), who studied two species, *Alcyomeum pallidum* and *Gorgonia cavolinii*. Two records only are given for each species, a small and a larger specimen having been compared in each case. In these experiments the total weight of the colony was taken as the basis of comparison without taking into account the proportion of inert skeletal material—the spicules in the first species and the spicules and chitinous axis in the latter.

Benedict (1915) has emphasized particularly the importance of the proportion of active protoplasmic tissue as shown even in the comparison of individuals of different sexes of the same species.

The observations herein recorded were made as part of a study of the ecological factors determining the distribution of Alcyonaria on the coral reefs of southern Florida. The data from which the amount of living tissue in the several species could be calculated were obtained three years ago in connection with a study of the importance of the alcyonaria as coral-forming organisms (Cary, 1915). A series of experiments were also carried out on the same species to determine their powers of resistance to increased temperature in order to discover whether or not there is any direct relationship between the rate of respiration and the temperature at which any species is killed; in other words, to determine whether the death of marine animals when subjected to high temperatures is in reality the result of asphyxiation, as Winterstein (1905) has maintained.

## EXPERIMENTAL.

The respiration chambers consisted of museum jars, with clamped tops fitting on rubber gaskets. The capacity of the several jars varied from 960 c.c., to 1,250 c.c. as was determined by weighing each one empty and again when filled with distilled water at a known temperature. In all experiments with Alcyonaria the displacement of the specimen was determined and subtracted from the capacity of the jar. Frequently, when it was desired to make several determinations at intervals on the same specimen a fragment of coral rock was allowed to remain attached to the specimen in order to keep it upright during

the period between experiments, as these organisms quickly become abnormal if allowed to lie prone on their side on the bottom (Cary, 1914, p. 86). The specimens were kept in a live-car in the intervals between the experiments, so that their condition was normal, as was shown by the fact that the colonies would remain in good condition in this live-car for at least two months.

The sea-water for each series of experiments was brought fresh from the ocean in large aquarium jars and the respiration chambers were filled by submerging them in the large jars. The temperature was controlled by placing the respiration chambers in an aquarium containing about 75 liters of sea-water. This aquarium was covered with a black box to exclude the light, as some of the species studied contained within their tissues enough symbiotic algæ (Zoöxanthellæ) to materially influence the results when the experiments were carried on in the diffuse light of the laboratory. This thermostat was connected with the running-water supply of the laboratory and during a 2-hour experiment (the usual duration) the temperature would not vary more than 0.2° C. On unusually hot days, when the temperature of the ocean-water over the shallow reef flats was subject to marked fluctuations, it was found that a much more even as well as lower temperature was obtained by cutting off the water-supply to the tank, as the early morning temperature of the water would then be maintained within half a degree throughout the day, while the variation during the time of a single experiment would not be measurable with a thermometer reading to 0.2° C.

The oxygen in the water was determined by the Winkler method, using the precautions as regards the purity of reagents described by McClendon (1917*b*). Before taking the sample for analysis at the end of an experiment the respiration chamber was inverted several times to insure complete mixing of its contents. An extended series of comparisons showed that there was no detectable difference in the results obtained by drawing the water sample—250 c.c. through a glass siphon into the empty bottle or when siphoning into a bottle by the displacement of mercury (McClendon, *l. c.*). The former, less complicated and much more rapid, method was therefore followed. The hydrogen-ion concentration ($P_H$) of each fresh supply of water was determined by a colorimetric method and the amount of $CO_2$ which it contained calculated from the $P_H$ and reserve alkali by a conversion table (McClendon, 1917*a*). In all the experiments it was found that so great a quantity of acid other than $CO_2$ was being given off that the values obtained for a respiratory quotient were far higher than would be obtained from the combustion of pure carbohydrates. Since the respiratory quotients were in every instance greater than unity, whatever the duration of the experiment, they have not been included in the table.

The results of all the experiments are summarized in table 1, in which the figures in columns 2 and 3 are the averages obtained from 5 determinations on specimens of various sizes of each species. *Briareum asbestum* has a central axis composed entirely of spicules, which in macerated specimens could not be certainly separated from those formerly contained in the cœnenchyma, so that both the skeletal masses are listed under the heading spicules.

TABLE I.

| Species of Alcyonaria. | Percentage of spicules. | Percentage of chitinous axial skeleton. | Percentage of living tissues. | $O_2$ consumed per kilogram of living tissue per hour. | Value of S/W. | Death temperature. |
|---|---|---|---|---|---|---|
| | | | | | | °C. |
| Briareum asbestum.. | 26.66 | 0.0 | 73.34 | 13.99125 | 3.25 | 38.2 |
| Eunecia crassa..... | 22.66 | 7.90 | 69.44 | 16.735 | 7.75 | 34.5 |
| Eunecia rousseaui... | 35.60 | 11.28 | 53.12 | 20.75846 | 2.18 | 35.0 |
| Plexaura flexuosa... | 30.66 | 5.10 | 64.24 | 16.6696 | 6.31 | 35.0 |
| Plexaura homomalla. | 27.41 | 6.72 | 65.87 | 35.5878 | 5.82 | 35.0 |
| Pseudoplexaura crassa | 21.84 | 10.18 | 68.34 | 44.0062 | 5.90 | 34.5 |
| Plexaurella dichotoma | 35.86 | 7.57 | 56.57 | 18.585 | 2.72 | 35.0 |
| Plexaurella sp?..... | 24.95 | 4.45 | 70.63 | 35.7084 | 4.73 | 35.0 |
| Gorgonia flabellum.. | 22.33 | 11.75 | 65.92 | 74.5900 | 9.40 | 37.0 |
| Gorgonia acerosa... | 19.75 | 7.08 | 73.17 | 54.9534 | 10.34 | 37.0 |
| Gorgonia citrina.... | 35.05 | 5.52 | 59.43 | 61.824 | 9.58 | 37.5 |
| Xiphigorgia anceps . | 25.83 | 8.33 | 65.84 | 68.40 | 12.60 | 37.5 |

Five observations were made in each case.

## DISCUSSION.

The validity of Rubner's (1885) hypothesis that heat-production (oxidation) is in direct proportion to the surface area of an organism has been denied by Montuori (1913) for all aquatic animals on the basis of his experiments recorded in that paper. On the other hand, Hoesslin (1888), Zuntz (1901), *et al.*, have maintained that their results on fishes support Rubner.

In Alcyonaria the surface in contact with the water varies greatly in different states of contraction or expansion of the colony. In the 12 species recorded in table 1 the surface area when expanded—all of them being able to completely retract their polyps—varied from 1.25 to 3.25 times that when the colony was in complete retraction. Since each species when undisturbed would arrive at complete expansion within a few moments after being put into the dark chamber, while on the other hand a slight agitation of the respiration chamber sufficed to cause them to remain contracted, the comparison of the consumption of oxygen under each of these conditions was a simple matter. While there were slight variations in the actual consumption of oxygen of any specimen in such a pair of experiments, the higher

metabolism occurred as frequently when the specimen had all its polyps completely withdrawn as when they were in full expansion.

Although the area of tissue exposed to the water had no constant effect on the rate of respiration, there was a striking relationship between the proportion of surface to weight of the several species and the rapidity of their respiration. As shown in column 6 of table 1, those species which have the greatest surface for a unit of weight $\left(\frac{\text{cm}^2}{\text{gms.}}\right)$ have by far the highest metabolism. The areas used in these calculations were determined accurately for each specimen by measuring the length and the diameter of each branch of a colony and treating them as cylinders or cones according to their shape. Under the conditions necessarily imposed while making the measurements, the colonies were always in a state of complete contraction, so that, when the specimens were in full expansion, the values of S/W would be from 1.25 to 3.25 times greater than those recorded in the table.

### RELATION BETWEEN DEATH TEMPERATURE AND RATE OF METABOLISM.

Column 7 of the table gives the temperatures found to be fatal to the different species on an exposure of 1 hour. When compared upon this basis the species studied fall into several groups; 2 of them succumb at 34.5° C.; another larger group finds the fatal temperature at 35° C., 2 others at 37° C., 2 at 37.5° C., while 1 species only could withstand temperatures up to 38.2° C. Although the last-mentioned species has the lowest respiration rate as well as the greatest power to withstand high temperature, there is no constant relationship between the death-temperature and the respiration-rate when all the species are compared. All of the species of the genus *Gorgonia* and the closely related *Xiphigorgia*, which have as a group the highest rate of respiration, are next to *Briareum* the most resistant to increased temperature. The two forms which are killed at the lowest temperature include *Eunecia crassa*, with next to the lowest rate of respiration, and *Pseudoplexaura crassa*, which stands eighth in the order of magnitude of respiration. Taken all together these observations offer no support to the hypothesis of Winterstein (1905), but on the contrary indicate that some other factor is the controlling agency in the ability of a marine organism to withstand high temperatures.

The heat experiments were performed in an open jar containing 6 liters of water and at the end of any experiment the amount of oxygen contained in the water was more than sufficient to allow respiration to go on in a normal manner if no other factor than oxygen tension were concerned. The acidity of the water at the close of the heat experiments was always greater than in respiration experiments carried on at 27.5° C. This may be only an expression of the abnormality of their metabolism at high temperatures, or have a causal relation to the death of the organism.

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X.

# MIGRATION OF INSECTS TO REBECCA SHOAL LIGHT-STATION AND THE TORTUGAS ISLANDS, WITH SPECIAL REFERENCE TO MOSQUITOES AND FLIES.

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# MIGRATION OF INSECTS TO REBECCA SHOAL LIGHT-STATION AND THE TORTUGAS ISLANDS, WITH SPECIAL REFERENCE TO MOSQUITOES AND FLIES.

By S. C. Ball.

## INTRODUCTION.

For the purpose of determining whether mosquitoes can, either by their own powers of flight or with the aid of favorable winds, migrate across the sea for considerable distances, the writer spent the period from June 26 to July 18, 1917, upon the Rebecca Shoal light-station. The work was undertaken under the auspices of the Carnegie Institution of Washington, Hon. G. R. Putnam, Commissioner of Lighthouses, having kindly granted permission to study at Rebecca Shoal light-house. Moreover Dr. L. O. Howard has kindly made timely suggestions respecting classification, but he is in no sense responsible for statements expressed herein. Except Stegomyia, the names of mosquitoes used are from Howard, Dyar and Knab, 1917.

The circumstances which suggested the desirability of such investigations were the repeated experiences of Dr. Mayer and other scientists at Tortugas, Florida, in connection with the occurrence there of mosquitoes. It appeared that these insects were abundant on Loggerhead Key only after northerly winds of several hours' duration—in other words, under conditions favorable to their migration from the mainland of Florida. Owing to the care which would be necessary in order to prevent absolutely the breeding of mosquitoes on the several keys of the Tortugas Group, particularly at Fort Jefferson on Garden Key, it was thought advisable to make observations at the nearest point to Tortugas where this difficulty could be overcome.

Rebecca Shoal light-station was chosen (1) because of its isolation from the mainland and other keys, and (2) because of its freedom from all except easily controllable breeding-places for mosquitoes. The lighthouse stands in 12 feet of water upon Rebecca Shoal, a small and entirely submerged part of the Florida Reef, 12 miles east of the Dry Tortugas and 48 miles west of Key West. The nearest point upon the mainland of Florida is Cape Sable, 105 miles northeast. Havana lies 95 miles to the south on the Cuban coast, while Cape San Antonio, at the western end of Cuba, bears southwest from Rebecca Shoal at a distance of 230 miles. Cardenas Bay lies 135 miles to the southeast.

Between Rebecca Shoal and Key West several keys of the Florida Reef intervene. Most important in relation to insect migration is the

Marquesas group. These keys are at the same time the largest and the nearest to Rebecca Shoal—24 miles east—and are largely covered with mangrove swamps which furnish breeding-places for myriads of mosquitoes. Their relation to the occurrence of these insects at the light-station will be considered later. In succession, passing eastward, lie Boca Grande, 6 miles distant from Marquesas; Man Key, Woman Key, Crawfish Key; then Mullet, Barracouta, Cottrell, and Snipe Keys at the entrance of Key West Harbor. It thus appears that any insect which reaches Rebecca light-station by flight alone must cover either 12 miles from Tortugas on the west or 24 miles from Marquesas on the east, or at least 105 miles from the mainland on the east and north, or 90 miles or more from Cuba.

The station consists of a wooden dwelling 25 feet square and 26 feet high, supported 34 feet above mean water-level upon an iron frame understructure. A 10-foot platform surrounds the base of the dwelling on all sides. The first story contains a single room 6 feet in height, which is occupied by four large wooden tanks for the storing of rain-water, and by a paint-closet and work-bench. The keeper's room, a kitchen, and pantry open into a small hall on the second floor. From here a stairway leads to the third floor, which is divided into a lamp and oil room, two assistants' rooms, and a hall. A ladder gives access to the lantern, light, and its mechanism at the top of the station. The lantern is surrounded by a narrow balcony. The diagonals of the station run north and south and east and west. At a level 8 feet above the water are two small boat-landings, one each on the southeast and northwest sides.

## MEANS BY WHICH INSECTS MAY REACH THE STATION.

There are four conceivable ways in which insects may reach Rebecca Shoal light-station. First by boat, for many are brought in provisions and other stores. Several species of larder pests, including two weevils and a flour beetle, two species of moths, one in flour and another in raisins, and an occasional fruit-fly, were observed on the station. The light-house power-boats usually bring on each trip a few house-flies and occasionally a blow-fly. In one instance a *Tabanus* was introduced.

It is extremely improbable that insects are attracted to the station from vessels which must pass through Rebecca Channel at a distance of at least 0.5 mile. Indeed none of the half dozen house-flies left the yacht *Anton Dohrn* on her voyage from Tortugas to Key West on July 30, although she passed within 100 yards of the Rebecca station. It is inconceivable that flies or mosquitoes voluntarily leave the solid support of a vessel where food is close at hand and its odors strong in order to land on a small light-station at a considerable distance. Anyone who has been on board ship at sea has probably observed how closely flies, beetles, dragon-flies, and moths keep to the vessel.

A second way by which insects may reach Rebecca Shoal light-station is through the agency of birds. Several species, including the man-o'-war bird, *Fregata aquila;* noddy, *Anoüs stolidus;* sooty tern, *Sterna fuscata;* and the royal tern, *Sterna maxima,* occasionally light upon the structure. It must be said, however, that no avian parasites were found at the station.

More important is a third method, the voluntary migration of insects from the mainland or from islands. It is conceivable that during calm weather such strong fliers as the Odonata, with certain Lepidoptera and Diptera, should voluntarily leave the Marquesas or Tortugas Keys and fly in a direction which would bring them within sight or smell of Rebecca Station.

Finally, there is the wind as an agent for the distribution of insects. It is well known that strong winds blow many Lepidoptera, Hymenoptera, Hemiptera, and Diptera out over large bodies of water, such as the Great Lakes and seas. That large numbers of these fall into the water and drown is evidenced by the masses of them washed upon the shores by the waves; but it is not known what proportion of the insects survive to reach other shores.

*A priori,* one would expect that the strong-flying species, such as the bees and wasps among the Hymenoptera, Sphingidæ of the Lepidoptera, and Tabanidæ among the Diptera, if driven by a high wind beyond sensing distance of land, would be more capable of sustaining themselves in the air and so of being carried to safety than the heavy-bodied, weak-flying insects like the Orthoptera and the flitting Lepidoptera. The habits of the latter accustom them to short flights and considerable periods of rest. Of mosquitoes, it must be remembered that, although they are comparatively small and not as a rule called on to fly long distances in search of food, still they are light in weight, have a relatively large wing surface, and are capable of sustaining themselves in the air for long periods. The same is true of other small Diptera, particularly the gnats.

Several long migrations of mosquitos have been recorded. In his book, "Mosquitoes," Dr. L. O. Howard cites two remarkable flights which were described in a letter to him from J. D. Mitchell, of Victoria, Texas. In October 1879, during a strong east wind which had been blowing for about 3 days, an immense swarm of mosquitoes migrated in a line 3 miles wide and 50 feet high from a marsh 35 miles to the eastward; 5 days were required for the passage. In 1886 a second swarm traveled 50 miles along the west shore of Matagorda Bay in such numbers that "they clouded the sky, bent down the grass with their weight, and made all driftwood and ground the same color."

Among the most important facts established by Dr. J. B. Smith and his assistants during their investigations of the mosquitoes of New Jersey in 1902–1904 were the length and frequency of the migrations

undertaken by the three species, *Aëdes sollicitans*, *A. cantator*, and *A. tæniorhynchus*. Breeding only in the salt marshes along the seashore, swarms of these three species migrate inland for distances of more than 30 miles; although capable of making these flights in calm weather, favorable sea breezes were found to hasten them.

As stated above, Dr. Mayer and others have noted in previous years that mosquitoes were abundant on Loggerhead Key only after the wind had been blowing from a certain quarter, usually the northeast or north, for a considerable period. Furthermore, a change of the wind into the east or west was always followed by a marked falling off in the numbers of mosquitoes encountered about the laboratory. The inference was that the northerly wind had blown large swarms of the insects away from the west coast of Florida and that part of them had reached Tortugas. If this inference were correct, even a small building, such as the Rebecca Shoal light-station, lying out in the ocean 18 miles east of Loggerhead, should form a sufficiently large support to attract a few mosquitoes which might be carried into its immediate vicinity. Even during a wind of such strength that the insects could not retain a foothold upon the windward side of the station, they would be able to do so under its lee.

## OPPORTUNITIES FOR BREEDING OF MOSQUITOES AT REBECCA SHOAL.

Obviously, in order to draw correct conclusions concerning the occurrence of mosquitoes and flies at an isolated point, it is essential that breeding-places there be under control. It was found that the only fresh water available to mosquitoes at the Rebecca Shoal light-station was contained in three sorts of receptacles; first, the four tanks on the lower floor for the storage of water obtained by draining through iron spouts the rain-water falling on the slate roof; second, the small depressions formed in the angles of the iron frame understructure; and third, the bilge-water contained in the two boats suspended from davits.

Concerning the small pockets and crevices in the steel frame of the structure, it is only necessary to state that all water which lodged therein was entirely evaporated by the sun in less time than would be required merely for the hatching of mosquito eggs. Since rains were infrequent in the period during which these observations were made, the possibility of a replenishment was precluded. It is conceivable that in a period of daily rainfall eggs deposited by mosquitoes in these depressions might develop and by good fortune yield a few adults. Still the rapid overflow during the characteristically heavy showers would doubtless wash out most, if not all, eggs and larvæ had they been present.

The storage tanks were accessible to mosquitoes since their covers did not fit closely; therefore it was necessary to be certain that no larvæ were present. Careful examination of the surface of the water

and of the contents on June 27 failed to reveal a single trace of larvæ, pupæ, molted skins, or adults which might have been drowned in the act of depositing eggs. Indeed, the lighthouse keepers, Mr. Lopez and his assistants, all of whom were familiar with the larvæ, agreed that they had never noted in water drawn from the tanks a single "wiggle-tail." Had larvæ been present they would probably have been detected, for the water is all drawn from the bottom of the reservoirs.

Owing to the ease and thoroughness with which frequent examinations of these tanks could be made, it was deemed unnecessary to treat the water surfaces with kerosene. Vigilance and daily examinations throughout the period of observations disclosed no sign of mosquitoes at any stage of their life-history in the reservoirs.

The third possible breeding-place (the boats), is also an extremely unfavorable one. In the case of the power launch a heavy film of lubricating oil is always present, while the sea-water in the bottom of the small dory, besides being too saline owing to evaporation, is also easily examined. No mosquitoes bred there.

From the above statement of conditions and the past experience of the keepers it is clear that mosquitoes rarely, if ever, breed at Rebecca Shoal light-station. Certainly none attempted to do so during the period covered by these investigations.

## CONDITIONS JUST PRIOR TO JUNE 26.

In order to account properly for the presence of certain insects found upon Rebecca shoal light-station on June 26 it is desirable to acquaint the reader with the conditions obtaining there in the period just preceding. From the lighthouse journal it was learned that on June 13 the keepers began painting the station, working that day upon the southeast side. At that time the wind was blowing freshly from the northeast. In other words, the air-current passed swiftly across the painted surface of the building; it was not on the lee side. Following several hours of calm on June 14 a light north wind sprang up and continued until June 15, when it became somewhat westerly, finally dying out, to be followed by 36 hours of calm.

It is of interest to note than on June 15 a coat of white paint was applied to the southwest side of the dwelling, and particularly that 100 or more small gnats were later found stuck in this paint. Now, it will be seen that this southwest face of the building was, in the period following the application of the paint, in the lee of the north and northwest winds; therefore, the insects seeking a resting-place on this surface were caught. Since they are not species that would have been brought in stores, it seems a fair conclusion that they were carried by the northerly wind from the coast of Florida. The possibility is not excluded that these gnats were brought to the station on the northeast breeze of June 13 and harbored there until the application of the paint.

On June 17, following the 36 hours of calm, a light northeast wind held until June 18, when it became north-northeast. During June 19 its direction was from the east. After a day's calm, on June 21, a light breeze blew from the northeast, while that side of the dwelling was being painted. Here a single insect was later found in the paint, a strong-flying damsel-fly which may have come down the wind and been able to make a landing, even though the air-current were sheering off across the surface painted.

An examination of the station on June 26 and 27 disclosed 6 living and 1 dead house-flies, *Musca domestica*, in the lower rooms; one mutilated damsel-fly and one pentatomid on the balcony beneath and outside the lantern, and three dead gnats on the sills of the storm panes inside. The gnats no doubt ascended from the dwelling below and had been unable to find their way out. In addition to these—which, in all probability, reached the station by flight—many larder pests were discovered, including two species of moths, one breeding in stale wheat flour and the other in packages of raisins, bean weevils (*Bruchus obtectus*) in dried beans, and a heavy infestation of weevils in two cases of the pilot bread which the keepers are required to keep on hand as a provision against want during possible prolonged periods of inability to secure their usual provisions from Key West. Each biscuit contained upward of two dozen larvæ and adults.

Upon inquiry of the keepers it appeared that on June 19 "one or two mosquitoes" had been observed by them in their living quarters, but that this was a rare occurrence. The wind on the two preceding days had been from the northeast and north-northeast, so that the source may well have been the coast of Florida. It is probable that had a careful lookout been kept at that time several other specimens would have been noted.

## METHODS OF OBTAINING INSECTS WHICH VISITED THE STATION.

On June 26 an insect net 5 feet in diameter and 6 feet deep was so suspended from the balcony railing beneath the lantern that any wind from the northeast, east, or southeast would spread it; but the hope that insects might be caught in this net was not realized during the entire period of observations. The lamp at this station is apparently not of sufficient strength and its flashes not of sufficient length to attract many of the insects which may be passing. During a revolution of the lamp and lenses lasting 30 seconds two groups of three similar flashes occur, each group requiring 9 seconds and being followed by a blank interval of 6 seconds.

Practically all mosquitoes and flies were taken with a hand net. In order to catch all of the former a close examination of the entire station was made several times a day in order to dislodge any which had found resting-places in dark corners. However, most of the mosquitoes

were taken in the act of biting some person. During a flight it was necessary only to station one's self quietly in the windward door of a room in order to entice any mosquito present within reach of the net. After it had been observed that these insects occasionally were attracted to the corks of bottles of raspberry shrub, dishes containing some of the liquid were set in several likely positions. Examination now and then resulted in the capture of a mosquito. After dark a flash-light was of great service in locating mosquitoes which were attempting to bite.

In order to capture house-flies it was necessary only to keep a close watch in the kitchen and living rooms and to net those which approached men at work outside. It was found possible to keep the station practically free of *Mucsa domestica* in this way. During periods of continued easterly winds the larger number of those taken on a given day were captured easily just after daybreak. These had doubtless arrived during the night. Single specimens would then be noted at long intervals during the day. Thus when dusk fell the station would again be practically free from flies.

It should be stated in this connection that there were absolutely no breeding-places for *Musca domestica* upon the station. The sewage and garbage were at once committed to the sea.

## INSECTS TAKEN AT REBECCA SHOAL FROM JUNE 26 TO JULY 18.

Those insects which migrated to Rebecca Shoal light-station proved to belong to four orders, Odonata, Neuroptera, Lepidoptera, and Diptera. Of the first order only two appeared, one being a large dragon-fly and the other a damsel-fly. A single Neuropteran, the golden-eyed lace-wing *Chrysopa*, was taken, while the only Lepidopteran was a moth, *Syntomeida epilais* Walker. The Diptera, as anticipated, were more numerous both as to species and individuals, and it is with these that the remainder of the paper will be mainly concerned.

On the next page is a table showing the weather conditions and the kinds and numbers of insects taken.

Considering first the occurrence of mosquitoes, the table on the following page shows that during all the time from June 26 to July 3, while the wind was blowing from the east or changing into the north, only a single mosquito was noted. This was taken on July 1 at 9 p. m., and was of the species *Aëdes niger*. It is probable that its point of departure was the Marquesas Keys, 24 miles to the east. A few others appeared later on east winds.

On July 2 the wind shifted into east-northeast and continued lightly from that direction during the night. At 5 a. m. of July 3 it was north, having shifted considerably during the night; at 10 a. m. it was northeast, at 12 noon it was north and continued so during the rest of the day, freshening toward night. The weather was now clear and the moon full. No mosquitoes were noted during the day.

At $5^h30^m$ on the morning of July 4 the wind was still in the north and continued so during the forenoon. Throughout the afternoon it blew from a few points west of north, again freshening toward night. At 8 a. m. the first specimen of what proved to be one of the two important mosquito migrations appeared at the station. This arrival, as may be calculated, was at least 27 hours after the wind had begun blowing from the northeast or north, but no more were noted until between 6 and $7^h30^m$ p. m., when 3 were taken, indicating that mosquitoes in the vicinity were increasing in number.

The wind was still blowing moderately from the north at $4^h30^m$ a. m. on July 5. That mosquitoes were still about was proved by the cap-

TABLE 1.—*Insects taken at Rebecca Shoal light-station and the conditions of their occurrence.*

| Date. | Winds. | | Weather. | Mosquitoes. | Musca domestica. | Other insects. |
|---|---|---|---|---|---|---|
| | Direction. | Strength. | | | | |
| June 26 | E. | Fresh.... | Squalls... | 0 | 6 | |
| 27 | E. | Moderate. | Do. ... | 0 | 2 | One green blow-fly, *Lucilia.* |
| 28 | E. | Do. .. | Do. ... | 0 | 0 | |
| 29 | E. | Do. .. | Do. ... | 0 | 0 | One *Tabanus.* |
| 30 | E. | Light.... | Clear.... | 0 | 0 | |
| July 1 | E. | Do. .... | Do. .... | 1 | 0 | One small gnat. |
| 2 | ENE. | Do. .... | Do. .... | 0 | 0 | |
| 3 $5^h00^m$ a. m. | N. | | | | | |
| $8^h00^m$ a. m. | NE. | Fresh.... | Do. .... | 0 | 0 | |
| $12^h00^m$ m. | N. | | | | | |
| 4 $5^h00^m$ a. m. | N. | Light.... | | | | |
| $4^h00^m$ p. m. | N. by W. | Fresh.... | Do. .... | 4 | 0 | |
| $9^h00^m$ p. m. | N. by W. | Do. .... | | | | |
| 5 $4^h00^m$ a. m. | N. | Moderate. | | | | |
| $5^h00^m$ p. m. | ENE. | Fresh.... | Do. .... | 21 | 0 | One dragon-fly. |
| $10^h00^m$ p. m. | E. by N. | | | | | |
| 6 $5^h00^m$ a. m. | E. by N. | Moderate. | | | | |
| $8^h00^m$ a. m. | ESE. | Do. .. | Do. .... | 2 | 25 | |
| $4^h00^m$ p. m. | NE. | Light.... | | | | |
| $8^h00^m$ p. m. | E. by N. | Fresh.... | | | | |
| 7 $5^h00^m$ a. m. | E by S. | Fresh.... | Cloudy... | | | |
| $9^h00^m$ p. m. | E. | Light.... | Clear.... | 0 | 5 | One *Tabanus.* |
| 8 $5^h00^m$ a. m. | E. | Do. .... | Do. .... | 4 | 5 | One blow-fly, *Lucilia.* |
| $12^h00^m$ m. | ENE. | Do. .... | | | | One blow-fly, *Lucilia.* |
| $8^h00^m$ p. m. | E. | Do. .... | | | | One neuropteran, *Chrysopa.* |
| 9 $2^h00^m$ a. m. | E. | Do. .... | | | | |
| $8^h00^m$ a. m. | NE. | Do. .... | Do. .... | 6 | 3 | One blow-fly, *Lucilia.* |
| $9^h00^m$ p. m. | NE. | Moderate. | | | | |
| 10 $5^h00^m$ a. m. | E. | Light.... | | | | |
| $4^h00^m$ p. m. | None. | Calm.... | | 0 | 0 | One blow-fly, *Lucilia.* |
| $8^h30^m$ p. m. | SE. | Strong... | Squalls... | | | |
| 11 $5^h00^m$ a. m. | WSW. | Fresh.... | Cloudy... | 37 | 18 | |
| $8^h00^m$ a. m. | SW. | Very light. | | | | |
| $9^h00^m$ p. m. | SW. | Do. | | | | |
| 12 $5^h00^m$ a. m. | ESE. | Fresh.... | Clear.... | 7 | 5 | Moth, *Syntomeida.* |
| $8^h00^m$ p. m. | ESE. | Strong... | | | | |
| 13 | E. by S. | Do. ... | Do. .... | 1 | 1 | |
| 14 | E. | Do. ... | Do. .... | 0 | 2 | |
| 15 | E. | Do. ... | Do. .... | 0 | 1 | |
| 16 | E. | Do. ... | Do. .... | 0 | 0 | |
| 17 | E. | Do. ... | Do. .... | 0 | 1 | |
| 18 | E. | Do. ... | Do. .... | 0 | 0 | |

ture of a specimen at this early hour, just as day was breaking. Another was taken at $5^h30^m$, and during the next 3 hours of the morning mosquitoes were so numerous that at times 2 or more could be captured with one sweep of the net; at $8^h15^m$ a. m. the count stood at 14 specimens. At intervals during the day others appeared, the last at 8 p. m., which made the total 21 for the day.

Now this marked increase in the number of mosquitoes encountered at the station, following a shift of 90° or more in the direction of the wind, from east to north by west, gains more significance as we note the interval of time elapsing between the inauguration of this change and the appearance of the insects. As already stated, at least 27 hours had passed from the time when, on the night of July 2 and 3, the wind was blowing from the vicinity of Cape Sable, 105 miles to the northeast on the southwest point of Florida, and the arrival of the first mosquito at Rebecca Shoal at 8 a. m. on July 4. That only 1 specimen was taken at this time indicates that comparatively few mosquitoes were blown out to sea from the southern capes. Not until toward night, after the wind had been blowing for over 37 hours, did the numbers begin to rise. The inference is that as the wind shifted—assuming that its direction held over the entire distance—points farther and farther north on the west coast of Florida contributed to the forced migration of mosquitoes. As will appear, the species taking part were only such as breed in salt marshes; therefore, those regions having such swamps would send out large swarms.

It will be seen that the body of the swarm encountered at Rebecca Shoal arrived on July 5, after the wind had been blowing from due north—the direction of Tampa Bay—for 48 hours or more. Obviously it can not be determined just how far up the coast these mosquitoes originated, but it is certainly possible that some of them may have come from points 150 miles to the north.

The specimens taken on this migration proved on determination to belong to two species. A single one of *Aëdes sollicitans* was captured on July 4. The other three, as well as the 21 taken on July 5, were of the species *Aëdes niger*. *A. sollicitans* and *A. tæniorhynchus* (a species closely allied to *A. niger*) have become noted for their migratory habits through the researches of Dr. Smith, of New Jersey. Breeding in the salt marshes along the seashore each summer develops immense swarms which spread inland to harass the inhabitants of cities even 30 miles away. In New Jersey *A. sollicitans* with *A. cantator* is the dominant species, *tæniorhynchus* being much less important, according to Dr. Smith:

> "*Culex tæniorhynchus* develops with *cantator* and *sollicitans* under the same conditions and migrates with them; but it does not fly so far and is always so much less abundant that it needs no special account here."

In the south, however, *A. niger* appears to be the dominant species and certainly flies, or is carried by winds, over the sea for long distances.

Late in the afternoon of July 5 the wind at Rebecca Shoal began to shift eastward, being east-northeast at 5 p. m. and east by north at $9^h45^m$, blowing freshly. The last mosquito was taken at 8 p. m. Daylight of July 6 still found the wind east by north and moderate. Two mosquitoes were captured, one at 5 a. m. and the second at $8^h27^m$ a. m., the last for the day. These individuals were, no doubt, the rear guard of those brought from Florida by the winds of the day preceding.

No more mosquitoes appeared until July 8, when 4 were taken during the forenoon; July 9 yielded 6 more, all *Aëdes niger*. Since the wind on July 7–8 and forenoon of July 9 was east—that is, it was blowing directly along the reef from Marquesas to Rebecca Shoal—the inference is that the mosquitoes were carried by the light breeze from these islands 24 miles away. Although there are extensive brackish swamps on the Marquesas Keys, it was found, when we visited them on July 30, that most of the water had evaporated, leaving only heavy mud. Rains had been infrequent during the preceding weeks with the result that swamps, which during the rainy season give rise to multitudes of mosquitoes, were during July unproductive. There were many adult *Aëdes niger* in the grass and among the mangrove trees, however, and it was no doubt from their ranks that the few brought on east winds to Rebecca Shoal were derived.

It was hoped that another north wind would arise, so that the striking migration observed on July 4 and 5 might be duplicated. While this did not happen, I was fortunate enough to be on the station during a period of southerly breezes which brought an even more marked flight of mosquitoes. After several hours of calm on July 10, southeast squalls blew up late in the evening, lasting for two hours. The wind then veered into the south and finally held west-southwest, blowing freshly all night. At $5^h30^m$ a. m. of July 11 the first mosquito was captured; 32 more were added to the collection during the day, and were well distributed as to time, 2 being caught at $7^h30^m$ a. m. and 1 at each of the following: $8^h15^m$, $8^h30^m$, $8^h52^m$, $8^h56^m$, $8^h57^m$, $9^h07^m$, $9^h08^m$, $9^h11^m$, $9^h16^m$, $10^h11^m$, $10^h24^m$, $11^h38^m$, $11^h40^m$, $12^h05^m$, $12^h10^m$, $12^h13^m$, $12^h15^m$, $1^h20^m$, $1^h22^m$, $1^h25^m$, $3^h30^m$, $4^h10^m$, and $5^h09^m$; between $6^h30^m$ and $7^h30^m$ p. m. 7 more were taken, but none was noted after darkness fell.

The greater number rose only to the platform level, but 8 reached the second story above, and 1 was caught by one of the assistant keepers while painting the railing above the lantern at the very top of the station, 65 feet above the water. In order to determine whether the insects were numerous just above the surface of the sea, I stationed myself on the boat-landing 8 feet from the water. One or two specimens were caught here attempting to bite, but they seemed no more abundant than at the level of the platform 30 feet above.

During the night of July 11–12 the wind veered again toward the east; at 5 a. m. July 12 it was blowing freshly from east-southeast; 7 mosquitoes appeared between 9 a. m. and $2^h20^m$ p. m.

Judging from the direction of the wind previous to and during this migration of July 11 and 12, we conclude that these mosquitoes were carried from the shores of Cuba. The time required for the passage was apparently less than in the earlier migration from Florida; at the end of only 10 hours after the wind, as noted at Rebecca Shoal, began to blow from the southeast—8 p. m. to $5^h30^m$ the following morning—the first mosquito appeared, whereas in the first case 27 hours were required. Since the strength of the wind was similar in the two cases this disparity in the time intervals may indicate that, while the second flight may have left the Cuban coast at the point nearest to Rebecca Shoal—95 miles directly south—the first swarm probably took its departure far up the west coast of Florida; for the nearest point, Cape Sable, is only 105 miles from Rebecca.

The fact that the great majority of mosquitoes taken belong to the single species *Aëdes niger* is evidence of its wide distribution and common occurrence in the south. Furthermore, this distribution is doubtless the result of the ability of these insects to sustain themselves in the air and so to be carried long distances across the sea by winds. Howard, Dyar, and Knab give the range of this species as the Antilles and Florida from Tampa southward.

On July 13 the wind, east by south early in the morning, finally settled into a strong and steady blow from due east and continued so through the next 6 days. A single mosquito taken on the morning of July 13 was the last which appeared during my stay at the lighthouse.

As Smith has shown, mosquitoes do not rise from the ground while strong winds are blowing. Had any been carried to the station it is improbable that they could have made a landing even on the lee side in the gale.

Very important, as supplementing my experiences at Rebecca Shoal, are observations made at Loggerhead Key by Dr. A. G. Mayer and other investigators. On July 11 they noted, under similar wind conditions to those at Rebecca Shoal, an unusual abundance of mosquitoes and preserved 22 specimens, which proved to be of the same species, *A. niger*. Dr. Mayer made the following record:

"On the night of July 10, at about 8 p. m., there was a sudden squall with rain from the southeast. By the morning of July 11 the wind was south to south-southwest, blowing in a gentle south-southwest breeze all day. Mosquitoes were noticed at about noon of July 11, and became a pest by night, so that we were unable to lie on the sand, as is our custom, at the southern end of the island. Many of them were also found in the laboratory, and they were thick in the bushes near the buildings and over the ocean about 300 feet from shore on the west side of the island. During the night of July 11 and 12 the wind veered to southeast to east-southeast, and the mosquitoes practically disappeared."

Thus it appears that the migration of July 11, occurring simultaneously at Rebecca Shoal and Loggerhead Key, presented a front of at least 20 miles. The individuals which actually alighted upon the station were, of course, only a small percentage of those which crossed the open sea within the visual radius of 13 miles; only those which came very close could have been attracted by any slight odors emanating from the lighthouse. Although Loggerhead Key is three-fourths of a mile long and hence much larger than Rebecca Shoal station, it still represents a small area on the surface of the sea. From these data one hesitates to compute the possible numbers of mosquitoes that were carried out to sea by the wind blowing from the Cuban coast.

On July 18, I was transferred from Rebecca Shoal to the Tortugas, where observations were continued. The wind held in the east for the 10 days of my stay there, so that no opportunity arose to witness another mosquito migration. Attention was turned toward a determination of the numbers and species of the mosquitoes still present on the islands, and their possible breeding-places.

As stated by Dr. Mayer, the veering of the wind on the night of July 11–12 caused a marked decrease in the numbers of mosquitoes encountered in the vicinity of the laboratory; still it was possible 10 days later to attract considerable numbers of *Aëdes niger* by stationing one's self quietly in the shade near the bay cedar bushes. On July 22 mosquitoes in one of the laboratories were so numerous that 4 were taken in one sweep of the net. Again on July 23, in the half hour just preceding darkness, 11 specimens were caught.

Since there are no swamps on the small sandy keys, the only breeding-places for mosquitoes are such receptacles as may be maintained or left by man. Examination showed that no larvæ were present in the fresh-water storage reservoirs at the laboratory or at the Loggerhead light-station. It was thought likely that mosquitoes might be breeding in cans thrown upon a waste pile among the bay cedar bushes. On investigation many were found that contained rain-water but no larvæ. In short, not a single larva was found on Loggerhead Key during my visit. Nevertheless, one small batch had, earlier in the season, matured in a shallow pool on a cement floor beneath the refrigerator, and the possibility is not excluded that *Stegomyia calopus* may have been breeding there late in July; several specimens of this species were captured about the laboratory. But that *Aëdes niger* or *sollicitans* were breeding at that time is extremely doubtful, for both require brackish water for their development, and all the receptacles contained only fresh water. Not only in the vicinity of the laboratory was it easy to obtain specimens; they were distributed over the entire key. In the early morning, afternoon, and evening *A. niger* could be attracted from the grass and bay cedar bushes.

The conditions on another of the Tortugas Islands are interesting in this regard. East Key lies 6 miles east of Loggerhead and is the

most isolated of the group as well as least frequently visited by man. Although it has a fairly luxuriant growth of bay cedars and xerophytic shrubs, there is not a drop of water on the key, and hence no possibility of mosquitoes breeding. On July 20 and 21 I found *Aëdes niger* so numerous at dusk and daybreak that as many as 4 females would be attempting to bite at one time. A walk through the grass at sunset was sure to arouse several of the insects. As to the origin of the mosquitoes found on East Key, two or three sources may have contributed. We have seen that on east winds a few of the *Aëdes niger* migrated to the Rebecca Shoal light-station. Since East Key is only 12 miles farther west it seems likely that a few may also reach this island from Marquesas, but, no doubt, the greater number came in the migrations of July 5 and 11. It is known that they are capable of living for some time in captivity, and so may well have survived on plant juices from July 11 to 21.

On July 23 an examination of the fresh-water reservoirs at Fort Jefferson was undertaken to determine the extent to which mosquitoes were breeding there. It was found that all except one of the tanks had been treated a short time before with kerosene, but this one contained large numbers of larvæ and pupæ. Several hundred were transferred in glass jars to Loggerhead Key, where some were preserved and the others allowed to mature.

Since *Stegomyia calopus* used to breed in the reservoirs at Fort Jefferson it was expected that at least a part of these would prove to be of that species. But all larvæ and adults reared from them proved to be *Culex pipiens* Linnæus. Not a single adult of this had been, or was later, taken either at Rebecca Shoal or at Tortugas. It is probable that the adults had been introduced by vessels visiting the fort and had deposited eggs in this reservoir. That the imagoes emerging from this source do not fly to other keys of the Tortugas 2 and 3 miles away is not surprising; *Culex pipiens* does not fly far from its breeding-place.

Unfortunately I did not succeed in determining the origin of the specimens of *Stegomyia calopus* which were taken on Loggerhead Key. The fact that the majority were males indicates that the breeding-place was not far away; indeed, it is known that this species seldom flies more than a few hundred yards.

## THE MIGRATION OF THE HOUSE-FLY.

The migratory powers of *Musca domestica* were clearly demonstrated by the occurrence of specimens at Rebecca Shoal. On my arrival at the station, June 26, I found 6 house-flies; 2 more were taken on the following day. As previously explained, there was no possible breeding-place for *Musca domestica* on the lighthouse; all refuse is immediately thrown into the sea. So it was plain that these flies had either been

introduced by boats or had flown across the sea. That boats are responsible for the presence of a few flies at the station was shown when the small auxiliary catboat brought one of the assistant keepers from Key West; 3 house-flies were found upon it as it was raised from the water to the platform. Mr. Roberts, the assistant, stated that the flies had annoyed him during the trip from the Marquesas Keys to Rebecca Shoal that day.

No more specimens were taken during the next 8 days, as will appear from the table on page 202. It is important to note that not even with the swarm of mosquitoes which arrived on July 5 were any house-flies noted. But on July 6, following the sudden change of the wind from north to east late on the preceding day, the lighthouse by contrast seemed fairly alive with *Musca domestica;* 25 were captured during the day—3 between 6 and $7^h30^m$ a. m.; 1 each at $9^h20^m$, $9^h40^m$, $10^h55^m$, $11^h30^m$, $11^h32^m$; 10 between $11^h33^m$ and $1^h15^m$; 2 at $2^h10^m$ p. m.; 1 at 3 p. m.; 2 at $4^h20^m$; 1 at $5^h15^m$, and the last at $5^h25^m$.

I am at a loss to account for the flight of house-flies from the east, since no such numbers had come to the station on the east winds which prevailed from June 26 to July 2. Had they arrived along with the mosquitoes on July 5 the obvious assumption would have been that they had come from the coast of Florida, but the fact that none appeared until 12 hours after the wind had veered into the east seems rather to point to Marquesas or some island farther east along the reef as their source. That it would have been possible, as far as distance is concerned, for the flies to have been carried from Key West 46 miles to the east, will appear after a statement of the conditions under which the second notable migration of *Musca domestica* appeared at Rebecca Shoal, but the reason for their leaving an eastern point in such large numbers at this time is still hidden; possibly the sudden change in the direction of the wind took them unawares.

During the 7th, 8th, and 9th of July the wind continued to blow lightly from the east. On the 7th of July, 5 flies were taken, 2 of them at $5^h30^m$ a. m.; 1 at 6 and 2 at $12^h30^m$ p. m. July 8 brought 5 more, 1 at $9^h40^m$ a. m.; 2 at $12^h30^m$; 1 at $2^h30^m$, and 1 at $5^h20^m$. A specimen was captured at $5^h10^m$ a. m. on July 9, another at $11^h30^m$, and a third at 6 p. m.; none appeared on July 10 while the wind was shifting toward the south, but on the memorable 11th, along with 37 mosquitoes, came 18 house-flies from Cuba. It is interesting to note that, whereas the mosquitoes were captured at all hours of the day as they reached the station, these flies were all taken between $9^h50^m$ and $11^h42^m$ a. m., 1 hour and 52 minutes. A possible explanation suggests itself. It will be remembered that no *Musca domestica* accompanied the mosquitoes from the coast of Florida on the north wind of July 4 and 5, but the very shortest distance in that direction is 105 miles. Now, the distance from Rebecca Shoal to the coast of Cuba is 10 miles less or about 95

miles. These facts, taken with the sudden appearance and disappearance of the flies on July 11, suggests that 95 miles is about the limit to the distance over which they were able to sustain themselves with the wind blowing moderately. That the wind was not the only factor that caused the cessation of their appearance is plain from the fact that it neither changed its direction nor lessened its rate until several hours later.

On July 12 the number of *Musca domestica* fell to normal, 5 being taken. During the succeeding days of high east winds very few appeared at the lighthouse, 1 on July 13, 2 on the 14th, 1 on the 15th, and the last on the 17th.

At Tortugas house-flies are numerous at all times during the season when the Biological Laboratory is open. An attempt was made to determine whether or not they breed there. Since all sewage and refuse is at once disposed of in the sea, it was thought possible that *Musca domestica* might be breeding in dead land-crabs. In order to test this source 100 house-flies were inclosed within a glass jar containing 3 inches of sand, 2 large ghost crabs, *Ocypoda arenaria*, and a small dish of water. The jar was tightly closed with fine bolting-cloth to prevent the entrance of ants. Apparently no eggs were deposited, for no maggots developed.

When it was found that there was little likelihood of house-flies breeding at Tortugas, attention was turned to the question as to whether it would be reasonable to expect that all *Musca domestica* found there had either been introduced upon vessels—and many certainly are—or migrated with the aid of the winds. Now, to one who had formed his estimate of the numbers of house-flies present on Loggerhead Key by observations made in the laboratories, such a proposition might well seem unreasonable, but as a matter of fact the flies are practically limited to the laboratories and to the lighthouse buildings. I found hardly a half dozen specimens in the bushy and untenanted parts of the island. True to their name, the house-flies seek the buildings occupied by man. It is probable that the *Musca domestica* on Loggerhead Key during the latter part of July numbered not over 5,000. Calculating the number which may be expected to have been attracted to the island on the southerly wind from Cuba on July 11, by multiplying 25 taken at that time on Rebecca Shoal light-station by the relatively larger size of Loggerhead—say 2,000—and we have 50,000 flies, a number greatly in excess of those present. Hence it seems entirely within the range of possibility that *Musca domestica* does not breed on Loggerhead or the other Tortugas Keys, but that the few thousand specimens found there migrate from the mainland or from larger islands. Account should also be taken of the few flies which may reach Tortugas from the east; as high as 5 per day were often borne to Rebecca Shoal on easterly winds.

## THE OCCURRENCE OF OTHER DIPTERA AT REBECCA SHOAL.

Besides mosquitoes and house-flies several species of Diptera visited Rebecca Shoal light-station during the period of observation. On June 29, with a moderate east wind blowing, a Tabanid of the sort commonly called greenheads settled upon the freshly painted railing of the platform, where it was captured; another was taken on July 7. Again the wind was blowing lightly from the east, indicating that these large flies were borne westward along the reef and were able to cross the 24 miles of open water between Marquesas and Rebecca Shoal station. *Tabanus* is not uncommon on Loggerhead Key.

Blow-flies of two species were also noted at the lighthouse and 5 were taken, 1 on June 27 and 2 on July 8, 1 on the 9th, and the last on the 10th. It will be seen from the table on page 202 that on all these days the winds were from the east.

The only other Dipteran which visited Rebecca Shoal was a small gnat taken just before dusk on July 2. Again the wind was in the east.

## OTHER INSECTS NOTED AT REBECCA SHOAL STATION.

Other orders of insects were but meagerly represented at Rebecca Shoal. As noted above, a single damsel-fly was caught in paint applied to the building on June 21. A large dragon-fly was seen to approach the station on July 5; it alighted on the roof of the lantern at the very top of the structure, and when an attempt was made to capture it with a hand-net it escaped and disappeared to the southwest. Although a lookout was kept for it throughout the rest of the day nothing further was seen of the specimen, thus indicating that its long flight from the northward had not exhausted its strength. One specimen of the Neuropteran called green-eyed lace-wing, *Chrysopa*, came to the station on July 8.

One Lepidopteran made the passage from Cuba to Rebecca Shoal on the southerly winds which were responsible for the flights of mosquitoes and house-flies. On the morning of July 12, I had just reached the platform on the southwest side of the station when a large moth alighted upon one of the davits. Its capture proved it to be one of remarkable beauty and strength, *Syntomeida epilais*. Its form, similar to that of the Sphingidæ, suggested such speed and endurance as might well sustain it over a flight of 95 miles.

## EVIDENCE THAT ODONATA AND LEPIDOPTERA MIGRATE TO TORTUGAS.

Mention has just been made of a dragon-fly which visited Rebecca Shoal station. At times these insects are numerous at Tortugas, both on Loggerhead and East Keys, where vegetation is abundant. In July 1914 within an hour I captured a score at East Key. On the island, whose extent is about 6 acres, there were at that time at least

100, but during the two days spent there the past season only 2 were seen, 1 of them being captured. At Loggerhead on July 19 a single individual was the reward of a day's lookout, and only 3 were seen there until the morning of July 30, when, as we were closing the laboratories preparatory to leaving the island, the air over the bay-cedar bushes near the buildings was alive with dragon-flies. I counted a score in sight at one time.

Now, since there is no possible breeding-place for Odonata upon any of the Tortugas Islands, it is plain that the great variation in numbers must be due to their migratory habits; for it is not likely that boats or other agencies are responsible for their introduction. As an example of the tenacity with which dragon-flies follow vessels upon which they may chance to be carried from shore, the case may be cited of a large specimen observed flying about the superstructure of the steamship *Concho* just before it left the dock at Key West. This insect, or one of its species, was noted on the following day while the boat was passing through the Straits of Florida. It was still on board when, toward the end of the voyage, the vessel was within 100 miles of New York.

Occasionally single specimens of Lepidoptera appear at Tortugas as if brought involuntarily from distant haunts. On July 28 a Sphingid, *Sesia tantalus* Linnæus, was captured while feeding on lilies near the laboratory. While certain species apparently breed on Loggerhead and East Keys, others are so rare as to indicate that they are immigrants. Dr. Mayer is authority for the statement that one of the larger Noctuidæ often comes to Tortugas on southerly winds from Cuba.

## DO SARCOPHAGIDÆ BREED AT TORTUGAS?

Conspicuous by their numbers on the open sandy shores and among the vegetation closely bordering them at Tortugas are two species of Sarcophagidæ or flesh-flies. Mr. R. R. Parker has identified the larger as *Sarothromyia femoralis* Schiner, and the smaller as *Sarcophagula occidua* Fabricius. Like most of the insects inhabiting these white beaches where the light is intense, both species are much lighter in color than ordinary members of the family. Their flight is also peculiar in so far as I am familiar with the group. As one walks along the beach these flies dart into the air only to alight a few feet in advance, repeating these short flights almost as a series of hops if disturbed by the progress of the intruder. I was unable to cause an extended flight. The possibility was suggested that their powers of flight had been modified after dwelling for some time on these isolated keys. If such were true then certainly they must be breeding there, for their numbers are considerable.

An experiment was performed in order to ascertain whether or not these Sarcophagids would breed in dead land-crabs. On July 19 a glass jar containing 3 inches of sand and a freshly killed ghost crab, *Ocypoda*

*arenaria*, whose carapace measured 1½ inches, was set under bay cedars near the beach and several specimens representing both species of flies were inclosed by means of a cover of fine bolting cloth. Within the next 2 days all the adults died and none was seen inside the jar until the morning of July 29, when three imagoes had emerged. On examination 101 pupæ were found near the bottom of the sand; the majority were of the larger species. It is thus evident that, if 104 maggots of a fly the size of the house-fly can develop to maturity within a single small crab, it is not necessary to look to migrations to keep up the stock of adults at Tortugas. To be sure, the large number of ants there may be relied upon to keep the flies within bounds; very few dead crabs are left long above ground. But years ago a former keeper of Loggerhead Light, Mr. George Billbury, called Dr. Mayer's attention to the fact that certain flies were to be noted about the entrances of crab burrows in the sand. As he surmised at that time, it is very possible that these flies may occasionally breed in crabs which, for some reason, die in their burrows.

## SUMMARY.

1. Large numbers of mosquitoes and house-flies are carried by northerly and southerly winds to Rebecca Shoal light-station and the Tortugas Islands from Florida and Cuba.

2. Easterly winds bring a few of these, as well as smaller numbers of blow-flies, horse-flies, and gnats from islands east on the Florida Reef.

3. Occasionally Odonata, Neuroptera, and Lepidoptera are carried by the winds to these parts of the reef.

4. Sarcophagidæ breed in land crabs at Tortugas.

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# XI.

# ON CHANGES IN THE SEA AND THEIR RELATION TO ORGANISMS.

By J. F. McCLENDON,

Associate Professor of Physiology, University of Minnesota Medical School.

Eight figures.

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# ON CHANGES IN THE SEA AND THEIR RELATION TO ORGANISMS.

By J. F. McClendon.

## PART I.

### INTRODUCTION.

The sea and air form the circulating media for the living organisms of the world, and although the air circulates so rapidly that no correlation between local faunas and floras and local composition of the air has been found, the local composition of the sea is distinctly affected by living organisms. The local changes in the composition of the sea are the subject of the present paper. These changes are due chiefly to organisms, but partly to meteorological causes. The circulation of the air certainly affects the sea, but the circulation is so rapid that my attempts at correlating meteorological observations (made for this purpose) with changes in the sea have not been encouraging.

The water evaporated is returned with addition of fixed nitrogen from electric discharges or falls on the land and is returned with various salts, chiefly $CaCO_3$, and with fixed nitrogen and other products of organisms. Various seaweeds absorb $CO_2$, thus leaving an excess of $CaCO_3$, which has a very low solubility and is constantly being precipitated in certain warm seas and is precipitated within the bodies of organisms in the surface waters of all seas. In working out the relation of H-ion concentration (pH) to the solubility of $CaCO_3$ in sea-water, I found that all sea-water is supersaturated with $CaCO_3$, and will lose some of it if shaken with calcite or aragonite crystals.

The study of the local changes in the sea is complicated by the presence of currents. The surface currents are due to winds, but, owing to the inertia of the water, they do not change as rapidly as the wind and hence are indicators of the prevailing winds (fig. 1), except where they are deflected by bodies of land or rotation of the earth. The largest currents may be constant (fig. 2), but the smaller currents show seasonal variations. Very few constant or seasonal vertical currents have been mapped, but vertical currents must be universal. McEwen has collected an enormous mass of evidence to show the presence of vertical

currents off the California coast. Vertical currents occur also off the coast of Norway and in the eastern Mediterranean in winter. I have found local and diurnal changes in the $O_2$ and $CO_2$ content of the sur-

FIG. 1.—Winds of the Atlantic Ocean. The long arrows show directions of steady winds, the short arrows the prevailing directions of variable winds.

face correlated with the presence of plants attached to the bottom (off the Florida Keys), indicating a complete inversion of the water or mix-

ing of top and bottom water several times a day; the mixing was not rapid enough, however, to equalize the temperature to the depth of 50 meters on a calm sunny day. Palitzsch (1912 *b*) found the average

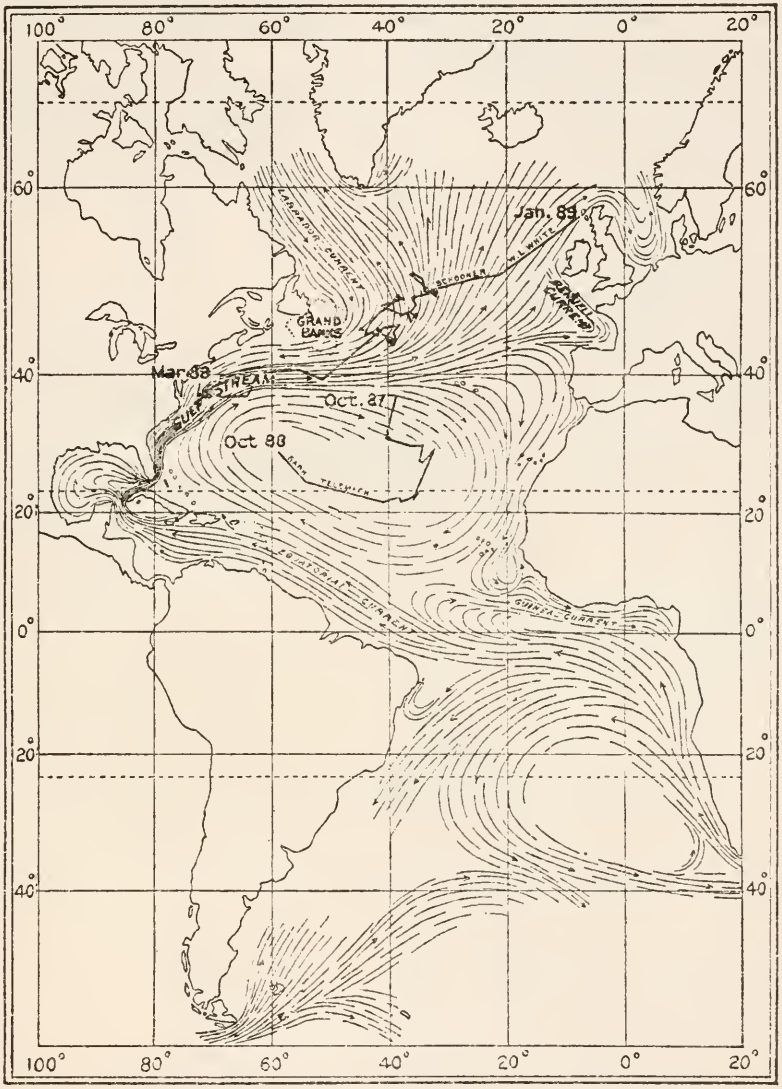


Fig. 2.—Currents of the Atlantic Ocean. The arrows show direction. The heavy lines are the courses of two derelicts, drifted by currents and winds.

$O_2$ in surface water of the North Atlantic to be 5.9 c.c. per liter during the day and 5.34 at night.

## METHODS.

The opportunities offered permitted of continuous observations at two stations, stations A and B, figure 4 (east and west of Loggerhead Key, Dry Tortugas), more or less systematized observations around Tortugas (fig. 4), and a series of observations on board between Tortugas and New York City (fig. 3).

The number of grams of chlorine per kilogram of sea-water (abbreviated Cl) was determined by titration with silver-nitrate solution, using potassium chromate as indicator and standardizing the whole method with sea-water standardized by the International Commission. The number of cubic centimeters of $O_2$ per liter was determined by the Winkler method. The self-closing water-bottle was not adequate for this purpose, but some observations were made on water drawn up from about 60 meters through glass and rubber tubing attached to the wire of a Lord Kelvin sounding-machine, and run continuously through the analysis bottle before reaching the pump. Twice the volume of the tube was run through the sample bottle with the least possible suction before the analysis was made. The alkaline reserve was recorded as the number of cubic centimeters of 0.01 N HCl used in titrating 100 c.c. of sea-water while boiling in a 500 c.c. Erlenmeyer "nonsol" flask, using di-brom-o-cresol-sulfonphthalein as indicator, until all trace of purple color had disappeared. The end-point is not sharp, but is sharper with this indicator than with any other yet found. The water must not dry on sides of flask. The pH was determined colorimetrically (McClendon, 1917), correction being made for Cl. The total $CO_2$ per liter was determined from the alkaline reserve and pH by means of the conversion table.

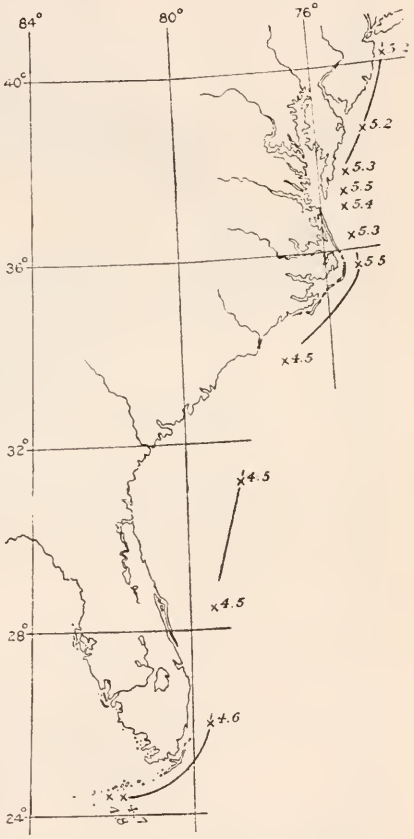


FIG. 3.—Oxygen in surface water taken on voyage from Key West to New York. The track of the steamer at night is marked by heavy black lines. The numbers denote the cubic centimeters of $O_2$ per liter at the stations marked $x$.

FIG. 4.—Positions of stations A to N at Tortugas, Florida. The numbers opposite the letters A to N denote the cubic centimeters $O_2$ per liter in the afternoon.

Table 1 gives the total $CO_2$ for alkaline reserve = 25.

TABLE 1.

| pH. | Total $CO_2$. | pH. | Total $CO_2$. | pH. | Total $CO_2$. |
|---|---|---|---|---|---|
| 8.17 | 45.0 | 8.26 | 43.65 | 8.35 | 42.29 |
| 8.18 | 44.9 | 8.27 | 43.5 | 8.36 | 42.14 |
| 8.19 | 44.7 | 8.28 | 43.35 | 8.37 | 41.99 |
| 8.20 | 44.55 | 8.29 | 43.19 | 8.38 | 41.80 |
| 8.21 | 44.4 | 8.30 | 43.04 | 8.39 | 41.75 |
| 8.22 | 44.3 | 8.31 | 42.89 | 8.40 | 41.60 |
| 8.23 | 44.15 | 8.32 | 42.74 | 8.41 | 41.45 |
| 8.24 | 44.00 | 8.33 | 42.59 | 8.42 | 41.30 |
| 8.25 | 43.8 | 8.34 | 42.44 | 8.43 | 41.15 |

The $CO_2$ of the air was determined colorimetrically (McClendon, 1917), 30 observations showing it to vary from 2.8 to 3.5 parts per

10,000. A new aneroid barometer was used and the mean value for 2 months was taken as 760. A thermometer graduated down to tenths of a degree was standardized by the United States Bureau of Standards and the other thermometers compared with it. A recording thermometer for the air was compared with the mercury thermometer, but the records were not found to be of much value in relation to the sea. Tortugas is about on the heat equator during July. There was a diurnal variation of the temperature of the air from 25° at dawn to 30° at 1 p. m., with a very slight upward drift during July and with a few variations due to storms. All time records are in local apparent time. The weights used were standardized by the United States Bureau of Standards and the glass apparatus and solutions standardized by weighing.

All water samples that could not be examined immediately were preserved in large flasks of resistance glass entirely full of the sample and were examined as soon as possible. Most of the samples taken at night were titrated by artificial light. The pH was in such cases determined with the aid of a "daylite" lamp, but the results were not very satisfactory.

Samples (for pH) taken a short time before sunrise were kept in nonsol flasks for the pH to be determined after sunrise.

The $CO_2$ tension at 30° was found from the pH, using table 2. The correction for other temperatures was made possible by the fact that a change of 1° temperature corresponds to 0.01 pH. The unit of $CO_2$ tension is one ten-thousandth of a normal atmosphere (760 mm. Hg) of $CO_2$.

TABLE 2.

| pH. | $CO_2$ tension. | pH. | $CO_2$ tension. | pH. | $CO_2$ tension. |
|---|---|---|---|---|---|
| 8.20 | 3.4 | 8.26 | 2.8 | 8.32 | 2.3 |
| 8.21 | 3.3 | 8.27 | 2.7 | 8.34 | 2.2 |
| 8.22 | 3.2 | 8.28 | 2.7 | 8.36 | 2.1 |
| 8.23 | 3.1 | 8.29 | 2.6 | 8.38 | 2.0 |
| 8.24 | 3.0 | 8.30 | 2.5 | 8.40 | 1.9 |
| 8.25 | 2.9 | 8.31 | 2.4 | | |

The sea-water was usually supersaturated or undersaturated with oxygen. The number of cubic centimeters of $O_2$ per liter at saturation at a given temperature was read from figure 5 and the excess or deficiency of saturation of the water was recorded. Figure 5 compares favorably with the results of Fox, who used a different method of analysis. Jacobsen's formula for cubic centimeters $O_2$ per liter at saturation is $10.062 - 0.2822\ t - 0.006144\ t^2 - 0.000061\ t^3 - 0.1073\ Cl + 0.003586\ tCl - 0.000055\ t^2Cl$. t = temperature and Cl = grams chlorine per kilogram of sea-water.

The determinations for constructing this curve were made as follows: A wash-bottle of about 500 c.c. capacity was supplied with about 400 c.c. of sea-water and immersed in a thermostat. Moistened outdoor air was drawn through the wash-bottle by means of a suction-pump until equilibrium was established. The air passed through a very small wash-bottle of sea-water and a copper coil (both immersed in the thermostat) before reaching the 500 c.c. wash-bottle. The analyses were made by the Winkler method, using the same standards as with the other determinations, a correction being applied for the average gas-pressure in the wash-bottle. No correction was made for the vapor tension of water, since it was the same as at the sea surface everywhere.

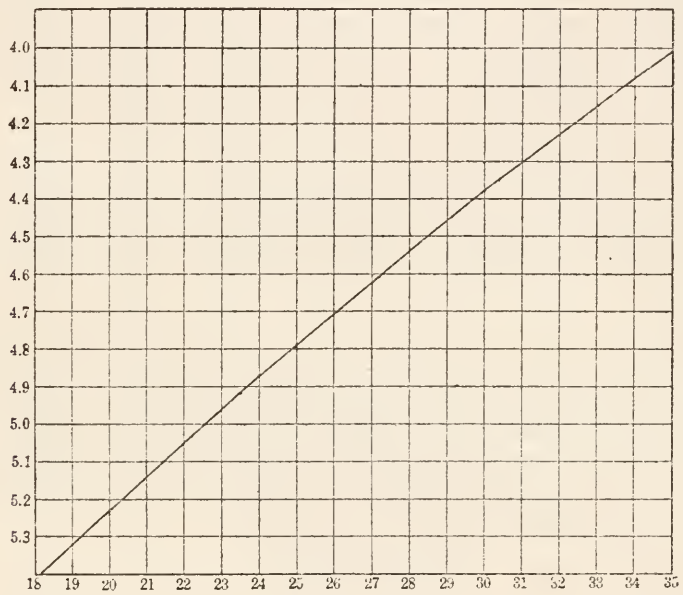


Fig. 5.—Curve of equilibrium of Tortugas sea-water with air at 760 mm. barometric pressure; the degrees temperature (18 to 35) are marked on the abscissa and the number of cubic centimeters of oxygen per liter of sea-water (5.3 to 4.0) on the ordinate.

## CURRENTS.

The surface currents to be considered are:

(1) The Gulf Stream, which parallels the Florida Keys and then flows toward Cape Hatteras (but only those observations between the latitudes of Miami, Florida, and Wilmington, North Carolina, were in the axis of the stream).

(2) The countercurrent in shallow water, which flows from Cape Hatteras, along the shore, until it reaches the Florida Keys, when it flows in the Hawk Channel (between the keys and the outer reef) and passes through the Tortugas and out into the Gulf of Mexico.

(3) The tidal currents. In the region of the Florida Keys the ebb is south and the flow north.

At Tortugas, the ebb flows through the northwest channel and continues out through the southeast and southwest channels, with a maximum speed of about 2 knots, as measured by Vaughan (1910, 1914), so that it does not go more than 12 miles before returning, and hence does not reach the Gulf Stream. But it seems probable that a considerable admixture of Gulf Stream water finally reaches Tortugas.

The time the tide turned, starting south (high water), at Tortugas is given in table 3 for July 1917.

TABLE 3.

| Day. | A. M. | P. M. | Day. | A. M. | P. M. | Day. | A. M. | P. M. |
|---|---|---|---|---|---|---|---|---|
| 1 | $5^h12^m$ | $7^h07^m$ | 12 | $2^h41^m$ | $3^h45^m$ | 22 | $10^h35^m$ | $11^h19^m$ |
| 2 | 6 02 | 7 56 | 13 | 3 42 | 4 59 | 23 | 11 12 | 11 49 |
| 3 | 6 53 | 8 35 | 14 | 4 41 | 6 04 | 24 | 11 52 | ..... |
| 4 | 7 42 | 9 15 | 15 | 5 38 | 6 39 | 25 | 12 11 | 12 41 |
| 5 | 8 32 | 9 54 | 16 | 6 29 | 7 46 | 26 | 12 38 | 1 53 |
| 6 | 9 21 | 10 34 | 17 | 7 18 | 8 28 | 27 | 1 17 | 3 25 |
| 7 | 10 14 | 11 16 | 18 | 7 57 | 9 06 | 28 | 2 16 | 4 47 |
| 8 | 11 08 | ..... | 19 | 8 43 | 9 42 | 29 | 3 28 | 5 51 |
| 9 | 12 01 | 12 07 | 20 | 9 16 | 10 16 | 30 | 4 41 | 6 43 |
| 10 | 12 50 | 1 14 | 21 | 9 59 | 10 49 | 31 | 5 45 | 7 26 |
| 11 | 1 43 | 2 28 | | | | | | |

## RECORDS OF ALL STATIONS AND OF A TANK OF SEA-WATER.

Table 4 gives the determinations of the surface water at station A (fig. 4) on the eastern side of Loggerhead Key for the month of July 1917, and table 5 gives similar data of a tank of sea-water 4 by 6 by 4 feet for July 23–24. The unit of $CO_2$ tension is one ten-thousandth of a normal atmosphere of $CO_2$ (760 mm. Hg).

TABLE 4, STATION A.

| Date. | Time of day. | Temp. | pH. | Total $CO_2$. | $CO_2$ tension. | $O_2$ per liter. | $O_2$ saturation, excess or deficiency. |
|---|---|---|---|---|---|---|---|
| July 2.. | $5^h00^m$ p. m. | 28.0 | 8.26 | 43.65 | 2.6 | 5.35 | +0.81 |
| 3.. | 8 30 a. m. | 26.7 | 8.18 | 44.9 | 3.3 | 4.5 | −0.15 |
| 3.. | 4 30 p. m. | 28.0 | 8.26 | 43.65 | 2.6 | 5.35 | +0.81 |
| 4.. | 6 30 a. m. | 27.6 | 8.20 | 44.65 | 3.2 | 4.52 | −0.06 |
| 4.. | 5 30 p. m. | 28.5 | 8.26 | 43.65 | 2.6 | 5.7 | +1.20 |
| 5.. | 6 30 a. m. | 27.8 | 8.22 | 44.30 | 3.0 | 4.52 | −0.04 |
| 5.. | 6 10 p. m. | 28.6 | 8.25 | 43.80 | 2.8 | 4.00 | +1.00 |
| 6.. | 6 30 a. m. | 27.9 | 8.20 | 44.55 | 3.2 | 4.55 | 0.00 |
| 6.. | 5 30 p. m. | 28.8 | 8.25 | 43.80 | 2.8 | 5.35 | +0.87 |
| 7.. | 6 30 a. m. | 27.7 | 8.19 | 44.70 | 3.3 | 4.44 | −0.13 |
| 7.. | 5 30 p. m. | 28.8 | 8.25 | 43.80 | 2.8 | 5.35 | +0.87 |
| 8.. | 6 30 a. m. | 27.5 | 8.20 | 44.55 | 3.2 | 4.3 | −0.25 |
| 8.. | 5 30 p. m. | 29.0 | 8.27 | 43.5 | 2.6 | 6.1 | +1.64 |

TABLE 4, STATION A—Continued.

| Date. | Time of day. | Temp. | pH. | Total $CO_2$. | $CO_2$ tension. | $O_2$ per liter. | $O_2$ saturation, excess or deficiency. |
|---|---|---|---|---|---|---|---|
| July 9.. | 6h30m a. m. | 28.1 | 8.20 | 44.55 | 3.2 | 4.26 | −0.27 |
| 9.. | 6 00 p. m. | 29.1 | 8.28 | 43.34 | 2.6 | 5.97 | +1.52 |
| 10.. | 5 30 a. m. | 28.2 | 8.20 | 44.55 | 3.2 | 3.96 | −0.57*a* |
| 10.. | 6 30 a. m. | 28.4 | .... | ..... | ... | 4.21 | −0.30*a* |
| 10.. | 8 30 a. m. | 28.8 | .... | ..... | ... | 4.47 | −0.01*a* |
| 10.. | 10 00 a. m. | 29.2 | .... | ..... | ... | 4.90 | +0.45*a* |
| 10.. | 11 00 a. m. | 29.6 | 8.25 | 43.8 | 2.9 | 5.2 | +0.79*a* |
| 10.. | 12 00 noon. | 29.5 | 8.25 | 43.8 | 2.9 | 5.2 | +0.78 |
| 10.. | 1h30mp. m. | 29.7 | 8.26 | 43.65 | 2.8 | 5.2 | +0.80*a* |
| 10.. | 3 15 p. m. | 30.0 | 8.26 | 43.65 | 2.8 | 5.6 | +1.22*a* |
| 10.. | 4 15 p. m. | 30.2 | 8.27 | 43.50 | 2.7 | 5.8 | +1.44*a* |
| 10.. | 5 15 p. m. | 29.5 | 8.27 | 43.50 | 2.7 | 5.5 | +1.08*a* |
| 10.. | 6 15 p. m. | 29.0 | 8.26 | 43.65 | 2.7 | 5.43 | +p.97*a* |
| 10.. | 7 00 p. m. | 28.8 | 8.26 | 43.65 | 2.7 | 5.13 | +0.65*a* |
| 10.. | 9 00 p. m. | 28.3 | .... | ..... | ... | 4.52 | 0.00*b* |
| 11.. | 2 50 a. m. | 28.1 | .... | ..... | ... | 4.25 | −0.28 |
| 11.. | 5 50 a. m. | 28.0 | 8.22 | 44.3 | 3.0 | 4.13 | −0.41 |
| 11.. | 6 30 a. m. | 28.2 | .... | ..... | ... | 4.20 | −0.32 |
| 11.. | 2 10 p. m. | 30.0 | 8.26 | 43.65 | 2.8 | 5.2 | +0.82 |
| 11.. | 4 30 p. m. | 29.5 | 8.26 | 43.65 | 2.8 | 5.3 | +0.88 |
| 12.. | 6 45 a. m. | 28.6 | 8.23 | 44.15 | 3.0 | 4.35 | −0.14 |
| 12.. | 12 15 p. m. | 30.5 | 8.25 | 43.8 | 2.9 | 5.3 | +0.96 |
| 12.. | 4 00 p. m. | 30.5 | 8.27 | 43.5 | 2.7 | 5.3 | +0.96 |
| 12.. | 5 00 p. m. | 30.2 | 8.27 | 43.5 | 2.7 | 4.97 | +0.61 |
| 13.. | 6 30 a. m. | 28.1 | 8.18 | 44.9 | 3.4 | 4.12 | −0.88*c* |
| 13.. | 12 30 p. m. | 29.5 | 8.25 | 43.8 | 2.9 | 4.85 | +0.43*c* |
| 13.. | 5 20 p. m. | 29.7 | 8.26 | 43.65 | 2.8 | 4.85 | +0.45*c* |
| 14.. | 5 45 a. m. | 28.3 | 8.20 | 44.55 | 3.2 | 4.5 | −0.02*c* |
| 14.. | 4 00 p. m. | 29.5 | 8.26 | 43.65 | 2.8 | 4.73 | +0.31*c* |
| 15.. | 6 00 a. m. | 28.2 | 8.21 | 44.4 | 3.1 | 4.14 | −0.39*c* |
| 15.. | 4 20 p. m. | 29.8 | 8.28 | 43.34 | 2.6 | 4.5 | +0.10*c* |
| 16.. | 6 45 a. m. | 28.0 | 8.21 | 44.4 | 3.1 | 4.4 | −0.14*c* |
| 16.. | 4 15 p. m. | 29.8 | 8.27 | 43.5 | 2.7 | 4.84 | +0.44*c* |
| 17.. | 6 25 a. m. | 28.0 | 8.20 | 44.55 | 3.2 | 4.33 | −0.23 |
| 17.. | 4 55 p. m. | 30.1 | 8.27 | 43.5 | 2.7 | 5.00 | +0.63 |
| 18.. | 6 00 a. m. | 28.0 | 8.20 | 44.55 | 3.2 | 4.28 | −0.26 |
| 18.. | 4 00 p. m. | 30.0 | 8.25 | 43.8 | 2.9 | 4.85 | +0.47 |
| 19.. | 5 20 a. m. | 28.1 | 8.21 | 44.40 | 3.1 | 4.30 | −0.23 |
| 19.. | 4 05 p. m. | 29.4 | 8.24 | 44.00 | 3.0 | 4.62 | +0.19 |
| 19.. | 4 30 p. m. | 29.3 | 8.24 | 44.00 | 3.0 | 4.84 | +0.44 |
| 19.. | 5 00 p. m. | 29.3 | .... | ..... | ... | 4.93 | +0.49 |
| 19.. | 5 40 p. m. | 29.7 | .... | ..... | ... | 4.87 | +0.43 |
| 19.. | 6 05 p. m. | 29.9 | .... | ..... | ... | 4.97 | +0.58 |
| 19.. | 6 30 p. m. | 29.7 | .... | ..... | ... | 4.84 | +0.44 |
| 19.. | 6 45 p. m. | 29.4 | .... | ..... | ... | 4.89 | +0.42 |
| 19.. | 9 35 p. m. | 28.6 | 8.22 | 44.30 | 3.1 | 4.45 | −0.04 |
| 20.. | 6 15 a. m. | 28.0 | 8.21 | 44.4 | 3.1 | 4.35 | −0.19 |
| 20.. | 6 20 a. m. | 27.9 | .... | ..... | ... | 4.40 | −0.15 |
| 20.. | 6 55 a. m. | 28.0 | .... | ..... | ... | 4.37 | −0.17 |
| 20.. | 8 25 a. m. | 28.4 | 8.22 | 44.30 | 3.0 | 4.58 | +0.07 |
| 20.. | 9 25 a. m. | 28.6 | .... | ..... | ... | 4.67 | +0.18 |
| 20.. | 10 30 a. m. | 28.9 | .... | ..... | ... | 4.58 | +0.11 |
| 20.. | 11 30 a. m. | 29.0 | 8.22 | 44.30 | 3.1 | 4.73 | +0.27 |
| 20.. | 12 15 p. m. | 29.2 | .... | ..... | ... | 4.70 | +0.25 |
| 20.. | 2 00 p. m. | 28.9 | 8.22 | 44.30 | 3.1 | 4.70 | +0.23 |
| 20.. | 3 30 p. m. | 28.7 | 8.22 | 44.30 | 3.1 | 4.70 | +0.22 |
| 20.. | 6 10 p. m. | 29.8 | 8.24 | 44.00 | 2.9 | 4.70 | +0.22 |
| 21.. | 5 45 a. m. | 28.0 | .... | ..... | ... | 3.94 | −0.60*d* |

*a* Unusually calm. *b* Sudden squall. *c* Rough weather. *d* Squall.

TABLE 4, STATION A—Continued.

| Date. | Time of day. | Temp. | pH. | Total $CO_2$. | $CO_2$ tension. | $O_2$ per liter. | $O_2$ saturation, excess or deficiency. |
|---|---|---|---|---|---|---|---|
| July 21.. | 6h30m a. m. | 27.9 | 8.20 | 44.55 | 3.0 | 4.12 | −0.43 |
| 21.. | 9 30 a. m. | 28.2 | 8.20 | 44.55 | 3.2 | 4.50 | −0.02 |
| 21.. | 11 40 a. m. | 28.7 | .... | ..... | ... | 4.63 | +0.15 |
| 21.. | 2 36 p. m. | 29.4 | 8.22 | 44.30 | 3.2 | 4.63 | +0.20 |
| 21.. | 4 30 p. m. | 29.1 | 8.22 | 44.30 | 3.1 | 4.61 | +0.16 |
| 21.. | 6 20 p. m. | 29.2 | 8.23 | 44.15 | 3.0 | 4.77 | +0.33 |
| 22.. | 5 20 a. m. | 28.2 | 8.22 | 44.30 | 3.0 | 4.13 | −0.39 |
| 22.. | 9 15 a. m. | 28.6 | .... | ..... | ... | 4.55 | +0.06 |
| 22.. | 2 30 p. m. | 29.6 | 8.25 | 43.80 | 2.9 | 4.76 | +0.35 |
| 22.. | 4 30 p. m. | 29.2 | 8.25 | 43.80 | 3.0 | 4.68 | +0.23 |
| 22.. | 6 15 p. m. | 29.0 | 8.23 | 44.15 | 3.0 | 4.60 | +0.14 |
| 22.. | 9 30 p. m. | 28.7 | .... | ..... | ... | 4.32 | −0.16 |
| 23.. | 5 40 a. m. | 28.2 | 8.20 | 44.55 | 3.2 | 4.07 | −0.45 |
| 23.. | 6 45 a. m. | 28.2 | .... | ..... | ... | 4.15 | −0.37 |
| 23.. | 8 45 a. m. | 28.7 | 8.21 | 44.40 | 3.2 | 4.62 | +0.13 |
| 23.. | 10 45 a. m. | 29.3 | 8.24 | 44.00 | 2.9 | 4.76 | +0.32 |
| 23.. | 12 10 p. m. | 29.9 | .... | ..... | ... | 4.77 | +0.38 |
| 23.. | 2 10 p. m. | 29.8 | 8.25 | 43.80 | 2.9 | 4.87 | +0.47 |
| 23.. | 3 55 p. m. | 29.5 | 8.25 | 43.80 | 2.9 | 4.81 | +0.39 |
| 23.. | 5 45 p. m. | 29.2 | 8.23 | 44.15 | 3.0 | 4.72 | +0.27 |
| 23.. | 7 10 p. m. | 28.9 | .... | ..... | ... | 4.55 | +0.08 |
| 23.. | 9 10 p. m. | 28.7 | 8.21 | 44.4 | 3.2 | 4.30 | −0.17 |
| 24.. | 2 30 a. m. | 28.5 | 8.21 | 44.40 | 3.2 | 4.15 | −0.35 |
| 24.. | 4 50 a. m. | 28.3 | 8.20 | 44.55 | 3.2 | 4.10 | −0.42 |
| 24.. | 5 40 a. m. | 28.3 | 8.20 | 44.55 | 3.2 | 4.15 | −0.37 |
| 24.. | 7 35 a. m. | 28.5 | 8.22 | 44.30 | 3.1 | 4.31 | −0.19 |
| 24.. | 12 40 p. m. | 29.8 | 8.25 | 43.80 | 2.9 | 4.88 | +0.48 |
| 24.. | 3 30 p. m. | 30.4 | 8.24 | 44.00 | 3.0 | 4.77 | +0.42 |
| 24.. | 4 45 p. m. | 29.9 | 8.23 | 44.15 | 3.1 | 4.76 | +0.37 |
| 25.. | 5 30 a. m. | 28.6 | 8.21 | 44.4 | 3.3 | 4.04 | −0.45 |
| 25.. | 10 00 a. m. | 29.0 | 8.22 | 44.3 | 3.3 | 4.60 | +0.14 |
| 25.. | 11 30 a. m. | 29.6 | 8.26 | 43.65 | 2.8 | 4.72 | +0.31 |
| 25.. | 12 15 p. m. | 29.8 | 8.26 | 43.65 | 2.8 | 4.72 | +0.32 |
| 25.. | 2 35 p. m. | 30.6 | 8.26 | 43.65 | 2.9 | 4.87 | +0.54 |
| 25.. | 4 20 p. m. | 30.3 | 8.26 | 43.65 | 2.8 | 5.29 | +0.93 |
| 26.. | 6 15 a. m. | 28.5 | 8.22 | 44.30 | 3.3 | 4.22 | −0.28 |
| 26.. | 12 40 p. m. | 29.4 | 8.24 | 44.00 | 3.1 | 4.86 | +0.43 |
| 26.. | 4 15 p. m. | 29.8 | 8.20 | 43.80 | 2.9 | 4.82 | +0.42 |
| 27.. | 6 40 a. m. | 28.3 | 8.20 | 44.55 | 3.5 | 3.82 | −0.70 |
| 27.. | 1 40 p. m. | 30.5 | 8.25 | 43.80 | 3.0 | 5.26 | +0.92 |
| 27.. | 3 50 p. m. | 30.7 | 8.25 | 43.80 | 3.0 | 5.06 | +0.73 |
| 28.. | 6 15 a. m. | 28.5 | 8.20 | 44.55 | 3.5 | 4.10 | −0.40 |
| 28.. | 1 30 p. m. | 30.5 | 8.26 | 43.65 | 2.8 | 5.10 | +0.76 |
| 28.. | 2 50 p. m. | 30.5 | 8.26 | 43.65 | 2.8 | 5.20 | +0.86 |
| 28.. | 5 45 p. m. | 30.2 | 8.27 | 43.50 | 2.7 | 4.78 | +0.42 |
| 29.. | 6 30 a. m. | 28.7 | 8.22 | 44.30 | 3.3 | 4.18 | −0.30 |
| 30.. | 5 30 a. m. | 28.8 | .... | ..... | ... | 4.42 | −0.06 |

TABLE 5, TANK.

| Date. | Time of day. | $CO_2$ tension of air. | Temp. | pH. | Total $CO_2$. | $CO_2$ tension. | $O_2$ per liter. | $O_2$ saturation, excess or deficiency. |
|---|---|---|---|---|---|---|---|---|
| July 23.... | $5^h40^m$ a. m. | 2.8 | 28.0 | 8.18 | 44.9 | 3.4 | 3.11 | −1.14 |
| 23.... | 6 45 a. m. | ... | 28.5 | .... | .... | ... | 3.43 | −1.07 |
| 23.... | 8 45 a. m. | 2.8 | 29.2 | 8.19 | 44.7 | 3.4 | 3.71 | −0.73 |
| 23.... | 10 45 a. m. | 2.8 | 30.0 | 8.21 | 44.4 | 3.3 | 4.08 | −0.30 |
| 23.... | 12 10 p. m. | ... | 32.5 | 8.21 | 44.4 | 3.5 | 4.50 | +0.31 |
| 23.... | 2 10 p. m. | 2.8 | 34.5 | 8.24 | 44.0 | 3.4 | 5.01 | +0.97 |
| 23.... | 3 55 p. m. | 2.8 | 35.2 | 8.26 | 43.7 | 3.3 | 5.25 | +1.25 |
| 23.... | 5 45 p. m. | 2.9 | 35.1 | 8.25 | 43.8 | 3.4 | 5.30 | +1.30 |
| 23.... | 7 10 p. m. | ... | 33.8 | .... | .... | .... | 5.07 | +0.98 |
| 23.... | 9 10 p. m. | ... | 32.5 | 8.22 | 44.3 | 3.4 | 4.76 | −0.57 |
| 24.... | 2 30 a. m. | ... | 29.7 | 8.21 | 44.4 | 3.3 | 4.36 | −0.08 |
| 24.... | 4 50 a. m. | ... | 28.6 | 8.20 | 44.6 | 3.3 | 3.30 | −0.19 |
| 24.... | 5 40 a. m. | ... | 28.5 | 8.18 | 44.9 | 3.5 | 3.26 | −0.24 |
| 24.... | 7 35 a. m. | ... | 28.7 | 8.20 | 44.6 | 3.3 | 3.48 | −1.00 |

Table 6 shows the determinations at stations B to P as located in figure 4.

TABLE 6.

| Station. | Day of month. | Hour. | Temp. | pH. | Total $CO_2$. | $CO_2$ tension. | Oxygen per liter. | $O_2$ saturation, excess or deficiency. |
|---|---|---|---|---|---|---|---|---|
| B | July 25.... | $10^h00^m$ a. m. | 28.9 | 8.22 | 44.30 | 3.3 | 4.26 | −0.21 |
| B | 25.... | 11 30 a. m. | 29.4 | 8.26 | 43.65 | 2.7 | 5.37 | +0.94 |
| B | 25.... | 12 15 p. m. | 29.6 | 8.27 | 43.50 | 2.7 | 5.51 | +1.1 |
| B | 25.... | 2 35 p. m. | 30.2 | 8.31 | 42.89 | 2.5 | 6.46 | +2.10 |
| B | 25.... | 4 20 p. m. | 30.0 | 8.33 | 42.59 | 2.2 | 6.29 | +1.91 |
| B | 26.... | 6 15 a. m. | 28.5 | 8.20 | 44.55 | 3.3 | 3.58 | −0.92 |
| B | 26.... | 12 40 p. m. | 29.4 | 8.25 | 43.80 | 2.9 | 4.91 | +0.48 |
| B | 26.... | 4 15 p. m. | 29.9 | 8.34 | 42.44 | 2.2 | 6.10 | +1.71 |
| B | 27.... | 6 40 a. m. | 28.2 | 8.18 | 44.90 | 3.4 | 3.33 | −0.19 |
| B | 27.... | 1 40 p. m. | 30.0 | 8.32 | 42.74 | 2.3 | 6.55 | +1.73 |
| B | 27.... | 3 50 p. m. | 30.6 | 8.35 | 42.29 | 2.2 | 6.81 | +1.47 |
| B | 28.... | 6 15 a. m. | 28.5 | 8.19 | 44.70 | 3.4 | 3.89 | −0.61 |
| B | 28.... | 1 30 p. m. | 29.9 | 8.32 | 42.74 | 2.3 | 6.18 | +1.79 |
| B | 28.... | 2 50 p. m. | 30.2 | 8.32 | 42.74 | 2.3 | 6.16 | +1.80 |
| B | 28.... | 3 30 p. m. | 30.5 | 8.32 | 42.74 | 2.4 | 6.28 | +1.94 |
| B | 28.... | 5 45 p. m. | 30.8 | 8.31 | 42.89 | 2.5 | 5.55 | +1.23 |
| B | 29.... | 6 30 a. m. | 28.6 | 8.22 | 44.30 | 3.1 | 3.87 | −0.62 |
| B | 30.... | 5 30 a. m. | 28.6 | .... | ..... | ... | 3.59 | −0.90 |
| C | 28.... | 3 30 p. m. | 30.5 | 8.32 | 42.74 | 2.4 | 6.28 | +1.94 |
| D | 28.... | 3 30 p. m. | 30.2 | 8.27 | 43 50 | 2.7 | 5.43 | +1.07 |
| E | 28.... | 3 10 p. m. | 29.3 | 8.24 | 44.00 | 2.9 | 4.53 | +0.09 |
| F | 28.... | 10 35 a. m. | .... | 8.23 | 44.15 | ... | 4.58 | ..... |
| F | 28.... | 3 40 p. m. | 29.3 | 8.24 | 44.00 | 2.9 | 4.46 | +0.02 |
| F | 29.... | 10 35 a. m. | .... | 8.22 | 44.30 | ... | 4.37 | ..... |
| G | 28.... | 9 00 a. m. | .... | 8.20 | 44.55 | ... | 4.05 | ..... |
| G | 28.... | 4 00 p. m. | 31.3 | 8.32 | 42.74 | 2.4 | 6.28 | +2.00 |
| H | 28.... | 4 20 p. m. | 34.6 | 8.43 | 41.15 | 2.0 | 6.81 | +2.77 |
| I | 28.... | 4 40 p. m. | 29.4 | 8.23 | 44.15 | 3.0 | 4.51 | +0.08 |
| J | 28.... | 4 55 p. m. | 29.5 | 8.24 | 44.00 | 3.0 | 4.84 | +0.42 |
| K | 28.... | 5 10 p. m. | 29.3 | 8.24 | 44.00 | 2.9 | 4.63 | +0.19 |
| L | 28.... | 5 22 p. m. | 29.5 | 8.25 | 43.80 | 2.9 | 4.72 | +0.30 |
| M | 28.... | 5 30 p. m. | 29.9 | 8.25 | 43.80 | 2.9 | 5.07 | +0.68 |
| N | 25.... | 4 10 p. m. | 29.7 | 8.30 | 43.04 | 2.5 | 5.45 | +1.05 |
| O | 18.... | 12 30 p. m. | 28.5 | 8.22 | 44.30 | 3.1 | 4.5 | 0.00 |
| [1]O | 18.... | 12 30 p. m. | 26.0 | 8.18 | 44.90 | 3.2 | .... | ..... |
| P | 20.... | 4 00 p. m. | 30.0 | 8.24 | 44.00 | 3.0 | 4.54 | +0.16 |
| [2]P | 20.... | 4 00 p. m. | .... | 8.24 | 44.00 | ... | 4.51 | ..... |

[1]Water collected at 50 meters depth. [2]Water collected at 65 meters depth.

In table 7 are given the determinations made on board, during the return from Tortugas to New York, together with the latitude and longitude of the stations.

TABLE 7.

| Date. | Lat. | Long. | Time of day. | Temp. | pH. | Oxygen per liter. | Cl per kilo. | Alkaline reserve. | $CO_2$ tension. |
|---|---|---|---|---|---|---|---|---|---|
| July 30.. | 24°36'N. | 82°48'W. | 9h00ma. m. | 29.0 | 8.21 | 4.48 | .... | .... | ... |
| | 24 36 N. | 82 41 W. | 10 00 a. m. | 29.6 | 8.21 | 4.59 | .... | .... | ... |
| | 24 35 N. | 82 35 W. | 11 00 a. m. | 28.2 | 8.21 | 4.80 | .... | .... | ... |
| | 24 35 N. | 82 34 W. | 11 10 a. m. | 27.7 | 8.21 | 4.80 | .... | .... | ... |
| | 24 34 N. | 82 28 W. | 12 noon. | 29.5 | 8.21 | 4.77 | .... | .... | ... |
| | 24 33 N. | 82 21 W. | 1h00mp. m. | 29.3 | 8.21 | 4.75 | .... | .... | ... |
| | 24 33 N. | 82 07 W. | 4 00 p. m. | 35.4 | 8.46 | 6.00 | .... | .... | ... |
| | 24 33 N. | 82 08 W. | 4 10 p. m. | 34.5 | 8.46 | 6.00[1] | .... | .... | ... |
| | 24 30 N. | 82 00 W. | 5 00 p. m. | 30.6 | 8.21 | 4.70 | .... | .... | ... |
| | 24 30 N. | 81 55 W. | 5 45 p. m. | 31.6 | 8.23 | 4.60 | .... | .... | ... |
| July 31.. | 24 33 N. | 81 48 W. | 5 00 a. m. | 30.6 | 8.21 | 3.96[2] | .... | .... | ... |
| | 24 33 N. | 81 48 W. | 12 40 p. m. | 31.7 | 8.20 | 3.93 | .... | .... | ... |
| | 24 33 N. | 81 48 W. | 3 30 p. m. | 31.2 | 8.21 | 4.82 | .... | .... | ... |
| | 24 20 N. | 81 30 W. | 6 30 p. m. | 29.3 | 8.22 | 4.73 | .... | .... | ... |
| Aug. 1.. | 26 10 N. | 79 40 W. | 5 25 a. m. | 29.2 | 8.21 | 4.58 | .... | .... | ... |
| | 28 26 N. | 79 20 W. | 3 00 p. m. | 29.8 | 8.21 | 4.5 | 9.9 | 25 | 3.3 |
| Aug. 2.. | 31 13 N. | 78 30 W. | 5 20 a. m. | 28.8 | 8.21 | 4.47 | 19.9 | 25 | 3.2 |
| | 33 40 N. | 77 00 W. | 3 00 p. m. | 28.8 | 8.21 | 4.47 | 19.9 | 25 | 3.2 |
| Aug. 3.. | 35 32 N. | 75 04 W. | 5 00 a. m. | 21.0 | 8.10 | 5.45 | 17.6 | 22 | 3.5 |
| | 36 18 N. | 75 20 W. | 10 30 a. m. | 25.4 | 8.19 | 5.25 | 17.1 | 22 | 3.0 |
| | 36 35 N. | 75 22 W. | 12 noon. | 25.2 | 8.19 | .... | .... | .... | 3.0 |
| | 36 52 N. | 75 22 W. | 1h30mp. m. | 24.6 | 8.19 | 5.35 | 16.7 | 22 | 3.0 |
| | 37 09 N. | 75 20 W. | 3 00 p. m. | 24.2 | 8.18 | 5.45 | 17.0 | 22 | 3.0 |
| | 37 32 N. | 75 15 W. | 5 00 p. m. | 23.4 | 8.16 | 5.25 | 17.4 | 22 | 3.1 |
| | 38 25 N. | 74 40 W. | 9 00 p. m. | 23.6 | .... | 5.14 | 17.2 | .... | ... |
| Aug. 4.. | 40 11 N. | 73 55 W. | 4 55 a. m. | 23.0 | 8.23 | 5.25 | 16.5 | 22 | 2.5 |
| | 40 14 N. | 73 55 W. | 6 30 a. m. | 22.6 | 8.22 | .... | 16.5 | .... | 2.6 |
| | 40 25 N. | 73 55 W. | 7 30 a. m. | 21.5 | 8.04 | .... | .... | .... | 4.2 |
| | 40 29 N. | 73 55 W. | 7 43 a. m. | 19.3 | 8.88 | .... | 15.4 | 21.5 | 4.5 |

[1]Inside Marquesas Lagoon. [2]Key West.

In figure 3 the stations from Key West to New York are marked by crosses and the appended numbers indicate the number of cubic centimeters of $O_2$ per liter. The track of the steamer during the night is marked by a black line and the track during the day is unmarked. Since the steamer had a speed through the water of about 12 knots, actual diurnal variations could not be determined. If, however, we assume that the Gulf Stream arises from a source of uniform composition, those observations in the axis of the stream should show the diurnal variations, except for the modifications due to local meteorological differences. Although *Trichosphærium* and other phytoplankton were present, and photosynthesis can occur at all depths less than 300 meters (light penetrating 1,000 meters), no marked or certain increase in $O_2$ in the sunshine was noted. At 5h20m a. m. August 2 there were 4.47 c.c. $O_2$ per liter and at 3 p. m. August 1 there was 4.50 c.c.; but no other pair of observations in the Gulf Stream shows a greater $O_2$

content in the afternoon than in the morning. Since oxygen is undoubtedly produced by these plants in the sunshine, the failure to observe an accumulation during the day probably lies in the fact that the temperature of the water rises about 1°, thus reducing the absorption coefficient for $O_2$ by 0.08 c.c. per liter and causing a passage of $O_2$ into the air. In contrast to this behavior of deep water, the $O_2$ concentration of the shallow water of Tortugas varied from 3 to 4.5 at about dawn to 4.5 to 7.0 at 3 p. m., the average maximum being shown in figure 4 opposite the station letters.

## DISCUSSION.

Determinations of the pH from certain North Atlantic stations, table 8, made by Palitzsch (1912 *b*) compare favorably with those I have made in the Gulf Stream and in the deep water near Tortugas.

TABLE 8.

| Depth, meters. | Sta. 80. 46° 17′ N. 7° 31′ W. 7 to 11 p.m. June. | Sta. 81. 41° 32′ N. 9° 32′ W. 4 to 6 p.m. June. | Sta. 84. 39° 22′ N. 9° 23′ W. 3 to 5 p.m. June. | Sta. 87. 37° 03′ N. 9° 15′ W. 1 to 5 p.m. June. | Sta. 91. 35° 53′ N. 7° 26′ W. 3 to 7 p.m. June. | Sta. 96. 35° 48′ N. 5° 58′ W. 9 to 11 a.m. June. | Sta. 97. 35° 50′ N. 5° 59′ W. 1 p.m. June. | Sta. 230. 35° 57′ N. 6° 00′ W. 11 a.m. September. |
|---|---|---|---|---|---|---|---|---|
| | *pH.* | *pH.* | *pH.* | *pH.* | *pH.* | *pH.* | *pH.* | *pH.* |
| 0.. | 8.20 | 8.22 | 8.22 | 8.26 | 8.24 | 8.20 | 8.24 | 8.24 |
| 10.. | .... | .... | 8.13 | .... | .... | .... | .... | .... |
| 25.. | .... | .... | 8.08 | 8.20 | .... | .... | .... | .... |
| 50.. | .... | 8.18 | .... | .... | 8.18 | .... | .... | 8.20 |
| 75.. | .... | .... | .... | .... | .... | .... | .... | .... |
| 100.. | 8.08 | 8.13 | .... | 8.13 | 8.13 | 8.20 | 8.20 | .... |
| 150.. | .... | .... | .... | .... | .... | .... | 8.15 | 8.15 |
| 200.. | 8.08 | .... | .... | 8.10 | 8.08 | 8.13 | 8.13 | 8.13 |
| 300.. | .... | .... | .... | .... | .... | .... | 8.10 | .... |
| 400.. | 8.06 | 8.04 | .... | .... | 8.04 | .... | 8.08 | .... |
| 500.. | .... | .... | .... | .... | .... | .... | .... | .... |
| 600.. | .... | .... | .... | 8.06 | 7.98 | .... | 8.07 | .... |
| 700.. | .... | .... | .... | .... | .... | .... | .... | .... |
| 800.. | 8.04 | 8.01 | .... | 8.04 | 7.95 | .... | .... | .... |
| 900.. | .... | .... | .... | .... | .... | .... | .... | .... |
| 1,000.. | 8.01 | 8.01 | .... | 8.01 | 7.98 | .... | .... | .... |
| 1,200.. | 7.98 | 7.98 | .... | 8.01 | 8.01 | .... | .... | .... |
| 1,500.. | 7.95 | 7.95 | .... | 8.06 | .... | .... | .... | .... |
| 2,000.. | 7.95 | 7.95 | .... | .... | .... | .... | .... | .... |

There is no increased amount of phytoplankton at Tortugas, but attached seaweed and symbiotic algæ and diatoms at the bottom cause the great diurnal change in $O_2$ concentration. On coral reefs the symbiotic algæ of corals and actinians are very effective, and in lagoons or other water which is not too agitated the symbiotic algæ of two species of the bottom medusa *Cassiopea* are a significant factor. One *Cassiopea xamachana* (11 cm. in diameter, weighing about 117 grams) in the sunlight gave out 1.9 c.c. $O_2$ per hour, whereas in the dark it

absorbed 2.8 c.c. per hour, showing that 4.7 c.c. per hour was produced by photosynthesis, at 30°. In other words, the $O_2$ given out in the day is about two-thirds the amount used at night.

The production of oxygen by plants by photosynthesis depends on a number of factors. The data found in the literature are all in terms of leaf surface and not volume or weight. Haberlandt found the capacity of the chloroplasts of different plants to be about the same—*i. e.*, the rate of photosynthesis per unit area depended on the number of chloroplasts per unit area, as shown in table 9.

TABLE 9.

| Plant. | Photosynthesis per unit area. | Chloroplasts per unit area. |
|---|---|---|
| Tropæolum majus... | 100 | 100 |
| Phaseolus multiflorus. | 72 | 64 |
| Ricinus communis... | 118.5 | 120 |
| Helianthus annuus... | 124.5 | 122 |

With the same plant, photosynthesis depends on temperature, light, and $CO_2$ supply, and a lowering of any one of these factors may make it the limiting factor (law of minimum). Blackman showed that photosynthesis is about doubled by a rise of 10° in temperature. He showed this to be true of temperatures as high as 45°, provided the rate immediately after raising the temperature was calculated. With injurious temperatures the rate constantly falls, and the initial rate was estimated by extrapolation of the time curve.

Blackman and Smith, working on fresh-water plants, showed that photosynthesis is about doubled by a rise of 10° in temperature and varies directly with $CO_2$ tension in the water and illumination. Their maximal values, reduced to 30°, were about as follows, in cubic centimeters $CO_2$ per square centimeter per hour: *Fontinalis* 0.149, *Elodea* 0.093, *Ceratophyllum* 0.245.

Most of the determinations were made with *Elodea* and some leaves overlapped, so that the average thickness was a little more than that of one leaf. If we assume a thickness of 0.1 mm. and a specific gravity of unity, 9,300 c.c. of $CO_2$ per kilogram per hour were consumed in photosynthesis (about 10 per cent of this was re-formed by respiration of the plant during the day and the same amount during the night, so that perhaps 9,000 c.c. was converted into oxygen for the use of animals). This is a maximum value and would be reduced in case of marine plants by decrease in light due to clouds, inclination of the sun, and absorption by the water. A very rapid use of $CO_2$ by seaweed causes a crust of $CaCO_3$ to form on the surface, thus keeping out light and $CO_2$.

The number of cubic centimeters of $O_2$ used per hour per kilogram by various groups of animals is shown in table 10 (Krogh's average of various species at 20°, and Montuori's at 25° as compared with my determinations and calculations at 30°).

TABLE 10.

| Group. | 20° | 25° | 30° | Group. | 20° | 25° | 30° |
|---|---|---|---|---|---|---|---|
| Jelly-fish | 6 | 53 | (12–75) | Cephalopods | 115 | 179 | (230–253) |
| Cassiopea | 13 | ... | 26, in the dark. | Other mollusks | 58 | 28 | (40–136) |
| Anthozoa | ... | 30 | (42) | Crustacea | 125 | 134 | (190–250) |
| Worms | 83 | 35 | (50–166) | Tunicates | 7 | 13 | (14–18) |
| Starfish | ... | 31 | (44) | Amphioxus | ... | 123 | (174) |
| Sea-urchins | ... | 19 | (27) | Fish | 110 | 177 | 590 (220–250) |
| Sea-cucumbers | ... | 14 | (20) | Reptiles | 92 | ... | (184) |

The discrepancies are due to differences in size, activity, and species. The calculations (in parentheses) were made on the assumption that the respiration at 30° is double that at 20° and 1.414 times that at 25°. A kilogram of the small fish I studied would use up all of the $O_2$ in 3,600 liters of the sea-water of the Gulf Stream in 24 hours. The respiration of the very active animals studied by others is about half as rapid and there is great variation with the species in sluggish animals.

With 1 kg. of fish in 300,000 liters of warm sea-water we should be able to detect a distinct fall in $O_2$ concentration during the night. In order to attain this effect there need be organisms, the equivalent of 1 kg. of fish, to 10 square meters of bottom in water 30 meters deep.

It will be seen from the foregoing sections that the changes in the sea that were considered are very complicated. If the dirunal curves are plotted they show secondary notches. It was thought probable that the secondary notches in the diurnal curves of the sea-water at station A might be due to horizontal and vertical currents and eddies. In order to exclude some of these currents the diurnal variation of a model lagoon was studied. A glass tank about 4 by 6 by 4 feet was placed in the open air and filled with sea-water and a few cassiopeas placed on the bottom. Convection currents stirred up the water in the tank, but there were necessarily no extensive horizontal currents over bottoms of different character and depth. The curves of the diurnal variations were smooth—that is, without secondary notches. The extremes (maxima and minima) of the curves were at about $5^h40^m$ a. m. and 4 p. m. The morning extreme was a little delayed, owing to partial shading of the tank for a short time, before and after sunrise, but there was a corresponding shading before sunset and therefore the curves were not skewed. The smooth curves obtained with the tank indicate that the notches in the diurnal curves at station A are due to currents in the water and not to technical errors. On partially cloudy days

it seems possible for clouds to make notches in the diurnal curves, and sudden squalls have a similar effect.

On July 10, 19, 20, 21, 22, 23, 24, and 25 very frequent determinations were made, so that the notches in the curves could be studied. With the omission of these small notches, the diurnal curves are plotted in figure 6. It may be observed that there was a general upward drift in temperature during July of about 2°. As a consequence of rise in temperature and increased cloudiness, there was a fall in the oxygen

Fig. 6.—Diurnal variation curves of sea-water from station A, Tortugas, during July, 1917. The date is marked on the right-hand border of the day interval, or where omitted it may be determined by counting the waves of the curve. The trough of the wave represents the early morning and the crest of the wave represents the early afternoon. The top curve represents the number of cubic centimeters $O_2$ per liter; the second curve, the excess or deficiency of saturation; the third curve, the number of cubic centimeters $CO_2$ per liter; the fourth curve, $CO_2$ tension; fifth, pH; and sixth, temperature.

concentration in the sea-water during July. July 10 was an unusually calm day (up to 9 p. m., when a brief squall appeared) and shows great extremes in all determinations. Contrasted with this are the windy days, July 13, 14, 15, and 16, during which the oxygen curves were very much flattened out. This shows that the oxygen content of the sea-water is somewhat influenced by the atmosphere. In figure 3 it may be observed that the oxygen content of the water north of Hatteras is increased with decreasing temperature and increasing absorption-coefficient, which is another demonstration that the oxygen content of the water is influenced by the air. On the other hand, shallow water is not nearly in equilibrium with the air in regard to oxygen. At

stations B and H samples of water were obtained which were 20 per cent undersaturated and 69 per cent oversaturated respectively.

Contrasted with the behavior of oxygen, no certain effect of the atmosphere on the $CO_2$ of the water as indicated by the pH was observed. At station A the oxygen curves were flattened out on July 13–15, due to high winds, but no flattening is observed on the pH or $CO_2$ curves. On going north into colder waters no fall in pH was noted, except on a very cloudy day at the mouth of the Chesapeake Bay and in the polluted water off New York Harbor, neither of which can be considered normal conditions. Palitzsch, however, noted that pH fell from 8.08 to 8.13, with more extreme drop in temperature in the North Atlantic and North Sea. This is not due to a difference in standards, since he found the pH of the Altantic at about 41° north latitude and of the Bay of Biscay to be 8.22 and 8.25 respectively.

No local effect of the $CO_2$ tension of the sea on the $CO_2$ of the air was observed. The wind reaching Tortugas blew over the Florida Keys and alternate areas of water of $CO_2$ tension = 3 to 3.5 in the morning and 2 to 3 in the afternoon. The $CO_2$ of the air varied from 2.8 to 3.5 without any relation to time of day. Part of this variation may have been merely the expression of technical errors, but a large number of duplicate experiments, and of experiments designed to show the limit of error, failed to support the idea that the variations were entirely due to technical errors. The $CO_2$ of the air was determined colorimetrically with 24 mm. sealed tubes containing the standards. The objection might be raised that the expanse of water of the same $CO_2$ tension was not great enough to affect the air and that considerable time was necessary to effect a change, and while one body of air was passing over the sea, both morning and afternoon variations in the water affected it alternately with neutralization of effects. The variations from day to day might have been due to slight shiftings of the wind and also to vertical currents in the air. In order to avoid such objections, Dr. A. G. Mayer made determinations over the Pacific Ocean. The standard tubes that he used were only 10 mm. in diameter, but the bicarbonate solution was kept in a gold-lined Jena flask and had not changed when tested on his return. The absolute standards may have been different from those used at Tortugas, but the method was adequate to show differences, provided equilibrium was always reached. The determinations were taken at noon each day, except where otherwise stated. The results of my calculations from his data are given in table 11.

From table 11 there probably may not be recognized any correlation between $CO_2$ tension of the sea and of the air. The cause for this may be that the apparatus was too crude or that exchange between air and sea is entirely masked by currents in the air. If we regard the air as sufficiently circulated to be of practically uniform composition, the changes in barometric pressure would not cause significant changes

in $CO_2$ tension and the latter might be considered constant. If there were sufficient exchange between sea and air the $CO_2$ tension of the sea would be practically constant. In table 11, the sea-water examined by Dr. Mayer on the trip from San Francisco to Hawaii (if we except the first station, where the water was polluted from land drainage and came in an insensitive region of the thymolsulfonphthalein tubes) had an almost uniform $CO_2$ tension, although the temperature rose 6.2°, thus necessitating in total $CO_2$ a fall of 1.3 c.c. per liter and rise in pH of 0.08. This may not, however, have been entirely due to exchange with the air *in situ*, but partly to the remote history of

Table 11.

| Date. | Latitude. | Longitude. | Bar. | $CO_2$ tension air. | $CO_2$ tension sea. | pH sea 20. | Temperature of sea. | Salinity. |
|---|---|---|---|---|---|---|---|---|
| Feb. 21.. | 36° 05′ N.. | 128° 38′ W.. | 756 | 3.1 | 3.1 | 8.05 | 12.3 | ..... |
| 22.. | 33 31′ N.. | 135 09′ W.. | 758 | 3.5 | 2.4 | 8.17 | 15.4 | ..... |
| 23.. | 30 53′ N.. | 140 53 W.. | 750 | 2.6 | 2.4 | 8.20 | 17.6 | ..... |
| 24.. | 27 49 N.. | 146 28 W.. | 762 | 2.4 | 2.4 | 8.23 | 20.1 | ..... |
| 25.. | 24 22′ N.. | 152 19 W.. | 763 | 3.0 | 2.4 | 8.25 | 21.6 | ..... |
| 27.. | 17 52 N.. | 159 13 W.. | 762 | 3.0 | ... | .... | .... | ..... |
| 28.. | 12 10 N.. | 161 17 W.. | 761 | 3.1 | ... | .... | .... | ..... |
| Mar. 1.. | 06 35 N.. | 163 21 W.. | 759 | 3.5 | ... | .... | .... | ..... |
| 2.. | 01 07 N.. | 165 30 W.. | 757 | 3.0 | ... | .... | .... | ..... |
| 3.. | 04 34 S... | 167 23 W.. | 757 | 3.5 | ... | .... | .... | ..... |
| 4.. | 10 14 S... | 169 14 W.. | 758 | 2.4 | ... | .... | .... | ..... |
| Apr. 19.. | 10 15 S... | 169 03 W.. | 757 | 3.0 | 2.8 | 8.24 | 27.8 | 35.10 |
| 20.. | 05 10 S... | 167 00 W.. | 756 | 4.1 | 3.6 | 8.15 | 26.8 | 35.41 |
| 21*a*. | 00 00 ... | 165 05 W.. | 756 | 2.9 | 3.7 | 8.12 | 25.0 | 35.26 |
| 22.. | 05 42 N.. | 163 12 W.. | 756 | 4.1 | 4.1 | 8.10 | 25.9 | 35.05 |
| 23.. | 11 19 N.. | 161 05 W.. | 758 | 3.0 | 2.7 | 8.22 | 25.4 | 34.58 |
| 23*b*. | 12 29 N.. | 160 39 W.. | ... | ... | 2.7 | 8.23 | 25.5 | ..... |
| 24.. | 17 03 N.. | 159 23 W.. | 760 | 2.9 | 2.8 | 8.21 | 24.5 | 34.58 |
| 25*c*. | 21 00 N.. | 157 50 W.. | ... | ... | 2.7 | 8.21 | 23.8 | ..... |
| 25*d*. | 21 10 N.. | 137 40 W.. | ... | ... | 2.8 | 8.20 | 23.9 | 34.94 |
| 26.. | 23 51 N.. | 153 44 W.. | 760 | 3.6 | 2.7 | 8.21 | 23.6 | 34.79 |
| 27.. | 27 18 N.. | 147 52 W.. | 760 | 3.5 | 2.5 | 8.23 | 21.6 | 35.05 |
| 28.. | 30 29 N.. | 141 50 W.. | 761 | 4.0 | 2.5 | 8.20 | 19.8 | 35.05 |
| 29.. | 33 39 N.. | 135 34 W.. | 762 | 3.1 | 3.1 | 8.10 | 16.6 | 33.89 |
| 30.. | 36 00 N.. | 128 59 W.. | 762 | 3.1 | 2.8 | 8.10 | 14.3 | 33.17 |
| May 1*e*. | 37 50 N.. | 123 25 W.. | ... | ... | 5.2 | 7.85 | 10.5 | 33.33 |

*a* $11^h00^m$ a. m. *b* $5^h00^m$ p. m. *c* $5^h00^m$ a. m. *d* $6^h00^m$ p. m. *e* $7^h30^m$ a. m.

the water. Pulitzsch has shown that the pH of the open sea decreases as the depth increases. It is well known that temperature decreases as the depth increases, and the two factors would have antagonistic effects on the $CO_2$ tension and tend to keep it constant. The reason for this stratification of the water may be that each stratum of water reached a certain temperature and $CO_2$ tension while at the surface, and the temperature effect on the density caused the superposition of the strata. After being buried out of reach of surface currents, the temperature and total $CO_2$ change very slowly and hence the $CO_2$

tension changes very slowly and may be practically the same when it reaches the surface the second time as when it left the surface the first time. Palitzsch's data are shown in table 8.

It is not intended to create the impression that the air regulates the $CO_2$ tension of the sea. There is 20 to 30 times as much total $CO_2$ in the sea as in the air. If there were no $CO_2$ in the air and this condition could be maintained by some external agent, all of the $CO_2$ in the sea would pass into the air, thus reducing the carbonates and bicarbonates to hydrates. In other words, the total $CO_2$ of the sea is available for regulating the $CO_2$ of the air. From the available data, however, it appears that the partial pressure of $CO_2$ in the air at sea-level is less than the average $CO_2$ tension of the sea. The reason for this anomaly is as follows: Part of the carbon fixed by photosynthesis at depths of less than 300 meters gravitates to greater depths and is oxidized, thus increasing the $CO_2$ content of deep water. Some of this deep water is constantly being carried to the surface by vertical currents, but on reaching the light the $CO_2$ is reduced again by photosynthesis and the original state of affairs is regained. Thus the sunlight interposes a barrier between the air and the main body of sea-water, so that the air contains less $CO_2$ than it would if the sea were more rapidly stirred.

Thus photosynthesis has an effect on the $CO_2$ of the air that is not entirely counteracted by the respiration of animals, because animals live not only at the surface but at all depths. The amount of photosynthesis must affect the $CO_2$ content of the air, but so many factors affect photosynthesis that probably no one factor is the limiting factor for the whole surface of the sea. Photosynthesis varies directly with both $CO_2$ tension and illumination, and either of these might become a limiting factor under certain conditions. There is an optimum pH range for plants, and since the temperature of the sea-surface as a whole is dynamically constant, there might be constructed an optimum $CO_2$-tension map of the sea. But the range of pH compatible with the life of seaweed is rather broad and may be different for different species and has not been worked out for the whole life-history of a single species, and besides, there may be some other limiting factor. It seems probable that the limiting factors are different in cold and warm seas. Photosynthesis is more than doubled by a rise of 10° in temperature, but the number of grams of plant tissue per square meter of sea surface is less in warm seas than in cold seas. The limiting factor in very cold seas may be temperature. The limiting factor at Tortugas may be fixed nitrogen, since I found less than 0.02 mg. of fixed nitrogen per liter of sea-water. There is a more abundant growth of eel-grass on the west side of Loggerhead Key than on the east, and sewage and garbage contaminates the water of the west side. On the other hand, the water of the west side is less agitated by the wind. At the Marquesas, fixed nitrogen is washed into the sea from decaying organic matter

on shore. There is an abundant growth of eel-grass in shallow water around Marquesas and in the lagoon where the water is not extremely shallow or perhaps disappears at low tide.

In the shallow pool between Bush Key and Long Key, Tortugas, blocked off from the sea except at extreme high tide by sand-bars thrown up in a recent hurricane, there is a dense growth of seaweed, which probably gets its fixed nitrogen from the adjacent shores. It seems probable that the fixed nitrogen formed by electric discharges, decomposition of organisms, and nitrifying bacteria that finds its way to Tortugas is so reduced by the action of Drew's bacilli as to be the limiting factor for the growth of seaweed. At any rate, the amount of phytoplankton per unit volume of sea-water is much smaller than in cold seas. Only on the bottom, and especially along shores where the plants may have access to fixed nitrogen (from the decay of organisms) before Drew's bacilli have had time to decompose it, do we find an abundant plant growth.

The limiting factor for animals seems to be food, but under some unusual conditions oxygen might become the limiting factor. Fish in an aquarium open to the air, and with a constant stream of oxygenated sea-water flowing in, suffocate if the stream of water is not sufficiently rapid. The same is true of sponges and other animals. If we take the lowest oxygen concentration found right at the sea surface, 1 kg. of fish would use all of the oxygen in 4,300 liters of sea-water in 24 hours and would show symptoms of altered metabolism before it was used up. Oxygen diffuses into the water from the air very slowly, and the fact that fish can come to the surface does not help them much. It seems improbable that fish would congregate in such numbers as to suffocate. On the other hand, dinoflagellates sometimes multiply or congregate in such numbers as to die and make the water foul. In the summer of 1907 I observed such swarms of *Gonyaulax polyedra* in the Pacific Ocean off La Jolla, California, that the water was red by day and turned to fire at night. The infected water welled up in spots which grew larger until nearly all of the water was infected. In about 3 days the water stunk and some dead fish were cast on shore by the waves. The death of large numbers of fish from unknown causes are reported by Taylor. It is not intended to imply that these were due to lack of oxygen, but the oxygen content of the water was not investigated and no satisfactory explanation was found.

No direct determinations showing absence of oxygen in sea-water have come to my notice, but $H_2S$ in the water is destroyed by oxygen and the presence of $H_2S$ indicates oxygen-lack. In some Scandinavian fjords $H_2S$ sometimes rises to within 4 feet of the surface and kills the oysters in "oyster polls." In the Black Sea $H_2S$ appears at a depth of 180 meters, according to Palitzsch.

# PART II.

## RELATION OF OXYGEN TENSION AND ACTIVITY OF THE NERVOUS SYSTEM TO METABOLISM IN CASSIOPEA.*

Henze (1910*a*) observed that sea-anemones use less oxygen when less is present in the sea-water, but interpreted this as due to the time required for diffusion into the animal. That is to say, he supposed that all of the cells were not supplied with oxygen when there was little in the sea-water. If oxygen was entirely absent in some of the cells, the decreased oxidation may have been merely the expression of the lesser number of cells taking part in the metabolism. Burrows showed that tissue cells require a certain oxygen tension for growth. Verzar showed that the cat's heart is slowed by reducing the oxygen, and Loeb and Wasteneys found that the heart-beat of *Fundulus* embryos may be slowed by reducing the oxygen. The growth of *Fundulus* may be suspended by lack of oxygen and may be slowed by diminishing the oxygen. Johansen and Krogh found that plaice-fish eggs develop slower when the oxygen tension is reduced.

The calorimeter consisted of either an 850 c.c. or a 900 c.c. Dewar flask (thermos bottle) inclosed in an air-tight container, which was immersed in water that was maintained at the same temperature as the water in the flask, within 0.003°. The technical difficulties were met as follows: Two Beckmann thermometers were adjusted and compared over the range of temperatures of the experiments and fitted with reading-lenses to estimate down to 0.001°. A large tank of sea-water was brought to 30° (which was about the temperature of the air) and its pH and $O_2$ and $CO_2$ content determined. A cassiopea was introduced into some of this sea-water that was dipped out into a jar. The thermos bottle, stopper, and thermometers were immersed in the large tank until they reached the temperature of the water. The cassiopea was transferred to the thermos bottle and a perforated cork stopper was inserted, with the exclusion of air-bubbles. One Beckmann thermometer was inserted through the perforation in the stopper and the other suspended in the tank, near the middle of the thermos bottle. A small hole, remaining in the stopper for exit of displaced water, was closed with wax. The pulsations of the cassiopea stirred the water inside the thermos bottle, and the water in the tank was mechanically stirred and was kept at the same temperature as that inside the thermos bottle by additions of small portions of warmer or colder water as required. The light was excluded by the silvering and coverings of the thermos bottle, but in some experiments in which a 900 c.c. glass jar with ground-glass cover was used in place of the thermos bottle, the light could be excluded by darkening the tank, so as to prevent

*The content of this section was published as a separate paper in Jour. Biol. Chem., 1917, xxxii, 275.

photosynthesis in the symbiotic plant cells. Time was measured by means of a stop-watch and a clock. The same cassiopea was used in a series of experiments.

The oxygen in the sea-water was determined by the Winkler method, which can be corrected for the small error due to a slight amount of organic matter given out by *Cassiopea*, and it was thought impracticable to use the complicated method of Shutzenberger and Risler (Henze, 1910*b*). A 250 c.c. glass-stoppered bottle was weighed empty and full of distilled water at a known temperature, in order to standardize its volume. It was fitted with a double-bored rubber stopper and a long and a short glass tube with rubber connections. The bottle was filled with mercury and the long glass tube was sucked full of the water to be analyzed and the stopper inserted. By inverting the bottle the sea-water was siphoned into it, when the rubber stopper was removed and the glass stopper inserted. The glass stopper was lifted and 1 c.c. of alkaline KI solution and 1 c.c. of 40 per cent $MnCl_2$ solution introduced (correction being made for this in the $O_2$ calculation) and the stopper was inserted. Colloidal membranes formed about the drops of alkali and violent shaking was necessary to break them. After the precipitate had settled, 2 c.c. of concentrated HCl were added and the stopper inserted and the bottle shaken. Its contents were transferred to a flask and titrated with 0.01 N sodium thiosulphate solution until the yellow color disappeared; then starch solution was added and the titration continued until the blue color disappeared; then the water was poured into the bottle and back into the flask and titrated until the blue color disappeared. The calculation was as follows:

$$\frac{0.056 \times \text{c.c. thiosulphate}}{\text{capacity of bottle} - 2} = \text{c.c. of oxygen per liter of sea-water}$$

and this quotient multiplied by 0.9 equals cubic centimeters of oxygen in calorimeter (on the assumption that the concentration of oxygen in the cassiopea was the same as that in the sea-water).

In order to reduce the carbonate content, the alkaline KI solution was made fresh every few days from two stock solutions. Carbonate-free NaOH solution was made by dissolving 100 grams of NaOH in 100 c.c. $H_2O$ in a glass-stoppered bottle and pipetting off after the carbonate had settled. One part of this was mixed with one part of 20 per cent KI solution before being used. NaOH made from metallic sodium contained a trace of nitrite and NaOH purified by alcohol contained but little more. This nitrite causes no error if the titration is quickly made immediately after adding the acid, but the contents of the flask slowly turn blue for hours after the end-point has been reached. If the acidity is greatly increased, however, the nitrite causes an appreciable error in the titration.

The $MnCl_2$ solution contained a trace of $Mn(OH)_3$, but this was removed by decantation. The thiosulphate was dissolved in $CO_2$-free

water and kept in an automatic burette with soda-lime tubes, and standardized with pure iodine. The starch solution was allowed to settle and only the clear upper portion used. When dextrins appeared in it a fresh solution was prepared.

Although pH determinations and $CO_2$ calculations were made in all experiments, it was found that the oxygen absorbed could be determined much more accurately than the $CO_2$ given out, and the $CO_2$ determinations are not listed with the experiments, but are collected together in the form of respiratory quotients. The respiratory quotients were 0.7, 0.74, 0.76, 0.84, 0.85, 0.86, 0.88, 0.9, 0.91, 0.92, 0.97, 0.99, 1, 1.02, 1.03, 1.1, 1.15, 1.2. It was impossible to tell whether the variation is due entirely to errors in the $CO_2$ determinations or whether the respiratory quotient varied. It is improbable, however, that respiratory quotients of 1.2 existed for even short periods of time, and these at least may be considered due to technical errors. According to Mayer (1914), *Cassiopea* lives on animal food exclusively and does not absorb carbohydrates from its symbiotic algæ, since it starves as rapidly in the light as in the dark. It may, however, get some carbohydrates from its animal food, or from glycoproteins during starvation. In this connection it may be of interest to note that *Cassiopea* secretes a mucin-like substance. Since the error in estimating $CO_2$ production may be 30 per cent in half-hour experiments with small cassiopeas, it is convenient to assume that the respiratory quotient is constant and is about 0.95, which is also the average found by Vernon for the hardier species of jelly-fish, on which he made most of his determinations.

The oxygen consumption is about doubled when the temperature is raised from 20° to 30°, and from results on other animals is probably an exponential function of the difference in temperature. Harvey (see Mayer, 1917) found the velocity of the nerve-impulse in *Cassiopea* to be a linear function of the temperature and to increase about 64 per cent on raising the temperature from 23° to 33°. I found the activity of the ganglia (rhopalia) in inducing pulsations of the umbrella to be about doubled with rise from 20° to 30° in temperature. The data are given in table 12.

TABLE 12.

| $O_2$ consumption. | | Temp. coeff. for 10° rise. | Pulsations per second. | |
|---|---|---|---|---|
| 20° | 30° | | 20° | 30° |
| 0.698 | 1.54 | 2.21 | .... | .... |
| 0.57 | 1.05 | 1.84 | 0.27 | 0.55 |

TABLE 13.

| pH. | $O_2$ concentration. | $O_2$ used. |
|---|---|---|
| 7.50 | 4.40 | 1.85 |
| 7.53 | 4.50 | 1.95 |
| 8.24 | 4.30 | 2.79 |
| 8.24 | 4.50 | 2.87 |
| 8.24 | 4.55 | 2.43 |
| 8.38 | 4.40 | 2.07 |
| 8.52 | 3.90 | 2.28 |
| 8.72 | 3.16 | 2.59 |

These experiments show the necessity of accurate temperature control, and in all of the other experiments in this paper the temperature

was measured to the nearest tenth of a degree and maintained to within 0.2° of 30°.

The sea surface is at about the optimum pH for metabolism (usually 8.1 to 8.3), but the variation in metabolism with variation of pH within the range studied is very slight, as shown by table 13 (diameter of cassiopea = 10 cm.).

These variations in oxidation may be due to experimental errors and variation in $O_2$ concentration, except the first two, which show a slight lowering of oxidation when the pH is reduced to about 7.5.

In comparing the rise in temperature in the calorimeter with that calculated from the $O_2$ consumption, the assumptions were made that the respiratory quotient was 0.95, and that a certain mixture of proteins, fats, and carbohydrates was burned, giving 6 gram-calories per cubic centimeter of $CO_2$, as in table 14.

TABLE 14.

| $O_2$ | $CO_2$ | Determined. | Calculated. |
|---|---|---|---|
| | | *gr. cal.* | *gr. cal.* |
| 2.18 | 2.07 | 12.6 | 12.4 |
| 2.54 | 2.41 | 16.2 | 14.5 |

In these experiments it was assumed that there was no loss of heat, although some heat must have passed into the thermometer bulb and glass lining of the thermos bottle. The specific heat of the sea-water and the cassiopea was taken as unity because the determinations were not accurate enough to warrant the application of small corrections. The experiments had to continue for 2 hours in order to obtain an accurately measurable rise in temperature, and the tedium of keeping the tank at the same temperature as the calorimeter necessitated the substitution of indirect calorimetry in the remainder of the experiments.

Some preliminary experiments to show the effect of $O_2$ tension are shown in table 15. Since the temperature was constant, the $O_2$ tension is proportional to $O_2$ concentration.

| | | | | | |
|---|---|---|---|---|---|
| Average $O_2$ concentration | 11.9 | 1.91 | :: | 3.36 | 1.55 |
| $O_2$ consumption | 2.6 | 2.38 | :: | 2.26 | 1.65 |

In performing these experiments, a number of possible sources of error were thought of and it was decided to make a more detailed study of the metabolism of *Cassiopea* before returning to the subject. The chief danger of error was in prolonging the experiment until all of the $O_2$ was used up. It was found that *Cassiopea* could live more than 7 hours without oxygen, in which case no measurable quantity of $CO_2$ was produced. Vernon observed practically no increase in the respiratory quotient of jelly-fish correlated with oxygen-want, whereas the respiratory quotient of fishes increased under these conditions.

In order to determine whether the rate of oxidation depends on the oxygen tension, it is desirable to know something about the oxygen tension inside the living cells. In other words, the transfer of oxygen to the cells must be facilitated as much as possible if we are to judge anything about the tension of $O_2$ within them from that in the sea-water.

This could be approximated by agitating free cells or a single layer of cells with the water or circulating the water over a single layer of cells. When using free cells, some are liable to injury and more or less disintegration, thus interfering with the titrations, but, notwithstanding the criticism of Heilbrunn, comparative results may be obtained (McClendon and Mitchell). *Cassiopea* was chosen because the cells are spread in thin layers on the surface of a mesoglea which will be shown to use practically no oxygen. The pulsations of a cassiopea bring currents of water over the cell-layers, so that diffusion is necessary only for a minute distance. The error due to this diffusion would be large only when the $O_2$ tension is very small. By skillful manipulation, the mucous secretion may be prevented from increasing or leaving the surface of the cassiopea.

Evidence that oxidation is confined to the cell-layers is apparent in the fact that oxidation is not proportional to the volume but to the surface. It would be practically impossible to measure the surface, but since the individuals are practically of the same shape, the surface is proportional to the square of the diameter. Since *Cassiopea* is elastic, the diameter was always measured under the same conditions, *i. e.*, resting on a glass plate, with the exumbrella in contact with the glass (and the average of 2 diameters at right angles to one another taken). Some rough preliminary determinations showed the $O_2$ consumption in cubic centimeters per hour to be about 0.023 time the square of the diameter in centimeters, as shown in table 15. Very small cassiopeas used more $O_2$ than calculated from the formula (an anomaly which is correlated with more rapid pulsations). A cassiopea 3.5 cm. in diameter pulsated once a second, whereas one 10 cm. in diameter pulsated 0.3 time per second. In order to compare experiments on *Cassiopea* where the weight is recorded, it is convenient to know that the diameter is cm. $= 2.25^3$ weight in grams.

TABLE 15.

| Diameter. | $O_2$ per hour. |
|---|---|
| *cm.* | |
| 3.5 | 0.4 |
| 7 | 1.4 |
| 8.5 | 1.17 |
| 9.5 | 2.16 |
| 10 | 2.7 |
| 11.5 | 2.78 |

Table 16 gives the respiration-rate under different conditions, except that the temperature is always 30°.

In this table the pH and $O_2$ per liter at the beginning of the experiment are given; the pH was about 0.09, while the $O_2$ was 1.5 c.c. lower at the end of each experiment. The average $O_2$ during each experiment influences the $O_2$ used per hour, but apparently no difference in the quotient of the $O_2$ used per hour divided by the square of the diameter can be correlated with difference in size. Using greater extremes of size, however, the quotient seems to decrease as the diameter increases, and therefore extreme sizes were usually avoided after this was discovered.

All of the experiments were made under conditions of starvation, and

hence the cassiopea used its own substance as a source of energy. Starvation can hardly be considered a pathological process in *Cassiopea*, however, since it may remain alive for months without food, constantly

TABLE 16.

| Diameter. | $O_2$ per hour sq. dia. | $O_2$ per liter. | pH. | $O_2$ per hour. |
|---|---|---|---|---|
| 7 | 0.0200 | 4.5 | 8.20 | 1.3 |
| 8 | .0187 | 4.2 | 8.22 | 1.26 |
| 8.5 | .0152 | 3.32 | 8.22 | 1.09 |
| 10 | .0287 | 4.5 | 8.24 | 2.87 |
| 10 | .0279 | 4.3 | 8.24 | 2.79 |
| 10 | .0243 | 4.55 | 8.24 | 2.43 |
| 10 | .0185 | 4.4 | 7.50 | 1.85 |
| 10 | .0195 | 4 5 | 7.53 | 1.95 |
| 10 | .0207 | 4.4 | 8.37 | 2.07 |
| 10 | .0228 | 3.9 | 8.52 | 2.28 |
| 10 | .0259 | 3.16 | 8.72 | 2.59 |
| 11 | .0230 | 3.54 | 8.17 | 2.79 |
| 11 | .0200 | 1.8 | 8.40 | 2.43 |
| 11 | .0160 | 1.57 | 8.02 | 1.93 |
| 11 | .0320 | 7.2 | 8.47 | 3.84 |
| 11 | .0400 | 7.44 | 8.46 | 4.87 |

decreasing in weight until it almost disappears before death. Mayer (1914) determined the loss in weight as about 5.6 per cent per day at about 30°, although no thermostat was used. If $y$ is the weight at any moment and $w$ is the weight when starvation commenced and $n$ is the number of days of starvation,

$$y = w(1-0.056)^n$$

Since I found the diameter to be 2.25 times the cube root of the weight, if the weight were 100 grams, the diameter would be 10.45 cm. The $O_2$ consumed during one day would be about 0.023 time the square of the diameter times 24 = about 60 c.c. $O_2$ absorbed and 57 c.c. $CO_2$ given out. If we assume that protein was burned and that 5.9 gram-calories correspond to 1 c.c. $CO_2$, the metabolism would equal 336 gm. cal. for the day. If we assume that a certain mixture of proteins, fats, and carbohydrates was burned and 6 calories correspond to 1 c.c. of $CO_2$, the metabolism would equal 342 calories per day.

Since I have shown that the metabolism is proportional to the surface and Mayer has shown that the loss in weight is proportional to the volume (weight), the composition of the cassiopea must change during starvation. In other words, it loses weight faster than it burns protein (or other organic matter), and hence the concentration of the protein must increase. Mayer (1914) found the cellular layer did not decrease in thickness during starvation, and Hatai found the percentage of nitrogen to the total body-weight increases during starvation and is also greater in small than in large, well-nourished cassiopeas. Therefore in attempting to calculate the metabolism from the loss in body-

substance, we should make it proportional to the loss in surface rather than loss in volume, since the loss in living matter seems to be proportional to the loss in surface and the cassiopea seems to have no other important store of food than its own protoplasm, the mesoglea apparently functioning chiefly as a skeleton.

Since the surface is proportional to the two-thirds power of the volume, we may assume that the protein is proportional to the two-thirds power of the weight (the density remaining practically constant). The protein equals 5.16 per cent of the two-thirds power of the weight (calculated from Hatai's data on the assumption that protein is 16 per cent N). The weight at the beginning of starvation was 100 grams and the protein 1.107 grams; at the end of one day the weight was 94.4 and the protein 1.07, being a loss of 37 mg. of protein. If we assume that 1 mg. of protein is equivalent to 4.4 cal., the metabolism the first day would be 163 calories, although I found it to be 336 to 342 calories.

Although these calculations are only approximate, since starvation is a little greater the first day than calculated by the formula, this great difference indicates that the burning of protein does not account for all of the heat. Since living cells contain lipoids or lipo-proteins and carbohydrates or glyco-proteins, it seems probable that proteins, carbohydrates, and lipoids are burned. The mesoglœa has not been analyzed separately, but is largely sea-water, with possibly a trace of glyco-protein. It probably has little calorific value, since the use of a store of food would cause a relatively greater metabolism in large starving cassiopeas than was actually observed.

Since the lining of the alimentary tract is not at the surface of the cassiopea and $O_2$ must diffuse through at least a millimeter of tissue to get to it, it was decided to pull off the manubrium and study the metabolism of the umbrella. The umbrella is disk-shaped, is covered on both sides by epithelium, and pulsates, thus circulating the water. The wound made by removal of the manubrium is of small area and is covered by an epithelium within a few hours, and the umbrella will live as long as a starving cassiopea. Some rough determinations indicate that the respiration of the umbrella is only about a fourth as great as that of the whole cassiopea. Table 17 records the measurements on 3 cassiopeas and on their umbrellas after removal.

TABLE 17.

| Diameter. | $O_2$ per hour ÷ (diameter)$^2$. | | Pulsations per second. |
|---|---|---|---|
| | Cassiopea. | Umbrella. | |
| *cm.* | | | |
| 3.5 | 0.033 | 0.0075 | 0.94 |
| 9.5 | .021 | .0041 | .58 |
| 11.5 | .030 | .0075 | .63 |

Since the respiration is influenced by the muscular activity or pulsation-rate, and the latter is not constant, it was decided to remove the ganglia (rhopalia) that induce the pulsations and start a continuous contraction-wave running around the subumbrella (the middle third of which has no neuro-muscular tissue, Mayer, 1908). The rhopalia were cut out by means of a cork-borer and the wave started by electrical stimulation. It was noticed, however, that the contraction-wave, apparently constant for short intervals of time, changed more rapidly at first and then more slowly, but never became absolutely constant, the change being perhaps associated with shrinkage of the umbrella. The effect of shortening and stretching on the contraction-wave was therefore studied. The rate of the contraction-wave depends on the rate of the nerve-impulse around the circuit of the nerve-muscle layer, but does not depend solely on the rate in the neuraxon, since there are numerous synapses, and furthermore, the path of the impulse is zigzag. Prof. L. R. Cary kindly showed me a stained preparation of the nervous network of the subumbrella. Concentric rings cut from the umbrella are capable of maintaining a trapped wave for some time, but if the ring is too narrow, the wave can not be started or soon ceases after being started. Trapped waves can be started in 2 or 3 concentric rings cut from the umbrella and the wave revolves about the inner ring more often per second than about the outer ring, but the revolutions per second are not in exact inverse proportion to the mean diameters of the rings or to the diameters of the inside tracks or holes in the rings. One subumbrella, 11.5 cm. in diameter, was cut into two rings and waves were trapped in them. The wave in the inner ring made 2.5 revolutions per second and the wave in the outer ring made 2 revolutions per second.

The uncertainty as to the length of the pace-making circuit that the nerve-impulse takes around the ring may be avoided by stretching the inner edge of the ring until it is of the same diameter as the outer, thus transforming the ring into a cylinder or belt. Such a ring can be stretched further and behaves in a strikingly reversible manner. Since Mayer (1917) has shown that the rate of nerve-conduction in *Cassiopea* depends on temperature and electric conductivity of the sea-water, it should be noted that all the experiments in this paper, unless otherwise stated, were made in sea-water of 30° and Cl = 20. Mayer found a variation of only about 2.5 per cent over the range of pH = 5.6 to 8.26, and this variation includes experimental errors and changes due to unknown causes. In the present experiments the pH was about 8.2 unless otherwise stated. The only difficulty in estimating the rate of the contraction-wave arose from the fact that the rate is 1 to 5 per cent faster in the ring that has just been stretched than in the ring that has just been relaxed, depending on the degree of recent stretching or relaxation. If, however, the circumference of the ring is allowed to

remain constant for 5 minutes after each short step of stretching or relaxation, the rate will approximate a mean value.

This behavior of the ring may be regarded as a form of hysteresis, since the number of revolutions per second of the contraction-wave tend to remain constant immediately after stretching or relaxation. I do not see how this can be explained on the assumption that the stretching of the neuraxon is the only factor, and it is significant to note that Carlson records no such hysteresis in the stretched nerve of the slug, where synapses are less numerous or entirely absent. One explanation of the increased rate immediately after stretching might be the thinning of the plasma membrane of the neuraxon, the regeneration in thickness taking appreciable time. Another suggestion is made that the immediate effect of stretching is increase in length of the neuraxon, but that this may be proportionately less than the increase in length of the strip of tissue, since the nerve-paths may be straightened, and that the apparent hysteresis is due to the possibility that after the nerve is stretched synapses gradually open, due to the tension, until the nerve-paths are proportionately as zigzagged as at the start. This supposition may similarly be applied to the fact that by prodding a cassiopea (having a trapped wave) with a stick, the number of revolutions of the wave per second is reduced, although no apparent increase in length of the conducting-path remains. The local stretching of the subumbrella with the stick might break some of the synapses.

Such complicated suppositions are not very useful, however, since they are not easily tested. A more probable hypothesis is given below in connection with the amplitude of the contraction-wave. The significant fact is that (ignoring the period of readjustment) the ring may be stretched until the circumference is increased 72 per cent with practically no change in rate (millimeters per second), although in order to accomplish this the number of revolutions per second or passages of the wave through the same tissue may be reduced 46 per cent. This is analogous to the effect of stretching a metallic wire on the passage of an electric current through it, with the difference that the process is completely reversible in *Cassiopea* after an increase of 84 per cent in length due to stretching. The results on two rings are shown in table 18, the rate being given in millimeters per second.

TABLE 18.

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Circumference.... | 223 | 263 | 283 | 286 | 306 | 326 | 346 | 366 | 386 | 406 | 426 | 446 | 466 | 486 | 506 | 526 |
| Rate ..... | 372 | 413 | 430 | 379 | 390 | 399 | 410 | 414 | 407 | 403 | 391 | 377 | 368 | 360 | 352 | 342 |

If the rate of wave propagation is the same, we would expect that in umbrellas of cassiopeas of different sizes the number of revolutions of the wave per second would be inversely proportional to the diameter. The diameter is measured before the wave is started and there

is a progressive shrinkage in the diameter, due to starvation and decrease in volume, tension of the regenerating tissue after removal of the rhopalia, and increased tonus of the musculature (sometimes transforming the disk into a cup-shape). This decrease in the diameter is associated with increase in revolutions per second, but agitation decreases the revolutions per second. It is therefore necessary to make the determinations under the same conditions for strictly comparative results. The determinations in table 19 were rough, but serve to indicate the general features.

TABLE 19.

| Diameter. | Revolutions of wave per second. | | |
|---|---|---|---|
| | Immediately. | After 24 hours. | After prodding with a stick. |
| *cm.* | | | |
| 9.75 | 2.38 | 2.50 | .... |
| 10.50 | 1.79 | 2.17 | 2.04 |
| 10.50 | 1.75 | 2.17 | 2.04 |
| 10.75 | 1.75 | 2.13 | .... |
| 11.00 | 2.38 | 2.08 | .... |
| 11.50 | 1.72 | 2.22 | .... |
| 11.50 | 1.79 | 2.22 | .... |
| 12.50 | 1.67 | 1.72 | 1.66 |
| 12.80 | 1.67 | 2.00 | .... |
| 13.50 | 1.61 | 1.67 | 1.40 |
| 13.50 | 1.61 | 1.79 | 1.52 |
| 14.00 | 1.67 | 1.79 | .... |

A comparison of these experiments with those on the actual velocity of the wave shows the circumference of the potential pace-making circuit to be about 1.8 times the diameter.

If the contraction-wave is stopped by pressure and after a rest of some minutes or hours is started again, it is slower than just before stopping, but if it is started again as quickly as possible after stoppage the rate is the same. This effect of a rest may be associated with nutrition or recovery from fatigue, since the amplitude of the contraction-wave is greater in the rested umbrella, although the number of revolutions per second is decreased. Whether the actual rate of propagation is changed would be difficult to determine. It seems evident that the wave of nerve-impulse precedes the wave of muscular contraction. The contraction of the muscle must stretch the adjacent regions, and hence stretch the region through which the nerve-impulse is passing, thus increasing the distance traveled in one revolution and decreasing the revolutions per second. When the amplitude of contraction is increased, the stretching of the nerves is increased and the revolutions per second are decreased, but whether this can account for the total decrease has not been determined. The speeding-up of the revolutions per second after the trapped wave is started is at first more abrupt and later more gradual, and is associated with both decrease in amplitude of contraction and decrease in diameter of the umbrella, due to starvation and contraction of scar-tissue.

Evidently a change in the number of revolutions per second of the trapped wave or the amplitude of the contractions would cause an error in the determination of the effect of $O_2$ concentration on metabolism, and in order to estimate the limits of such errors the relative metabo-

lism of the muscle and other tissues was studied. The umbrellas of 3 cassiopeas, *a*, *b*, and *c*, of the same size (diameter = 11.5 cm.) were used (each for a series of experiments). In some experiments the rhopalia remained and the normal pulsations were generated, in others a trapped wave was induced, and in others the subumbrella was removed or merely the mesoglœa left. The apparent (but slight) metabolism of the mesoglœa was probably entirely due to a few remnants of epithelium and to bacteria, which always attack the mesoglœa when the epithelium is removed. At any rate, the metabolism of the mesoglœa is too small to be of significance. The pH was 8.2 and the $O_2$ per liter 4.5 c.c. at the beginning of each of the experiments.

Table 20.

| Individual. | $O_2$ per hour. | Parts of umbrella used. |
|---|---|---|
| *a* | 0.86 c.c. | Umbrella with 0.64 pulsation per second. |
| *a* | 0.97 | Umbrella with 0.64 pulsation per second. |
| *a* | 0.158 | Mesoglœa + exumbrella only. |
| *b* | 1.12 | Umbrella with trapped wave, 1.47 per second. |
| *b* | 1.08 | Umbrella with trapped wave, 1.47 per second. |
| *c* | 0.5 | Umbrella not pulsating. |
| *c* | 0.6 | Umbrella not pulsating. |
| *c* | 0.03 | Mesoglœa + bacteria. |
| *d* | 0.88 | Umbrella with 0.7 pulsation per second. |
| *d* | 0.7 | Umbrella not pulsating. |

The removal of the rhopalia in the umbrellas with trapped waves or without pulsations reduced but slightly the amount of tissue. If we take the metabolism of the normal pulsating umbrella at 100, the exumbrella is about 14 and the resting subumbrella 60, with an addition of 26 for normal pulsations or 65 for trapped wave. Therefore, the neuro-muscular tissue may perform about 26 to 46 per cent of the metabolism, and changes in rate or amplitude of the contraction-wave are to be avoided as much as possible.

In subsequent experiments, the manubrium and rhopalia were removed from the cassiopea and a C-shaped cut was made through the neuro-muscular layer, about one-third the radius from the outer margin of the umbrella, and a trapped wave was induced by stimulation near the outer margin. The wave passed around the outer part of the subumbrella, and each time it passed the opening of the C it spread to the inner part, dividing into two equal waves, meeting on the far side with mutual destruction. In this way the outer part, in which the trapped wave was first induced, was made pacemaker and the result was a more permanent wave. The wave causes circulation of water against all parts of the epithelium except a small portion of the exumbrella which has a very low metabolism. If the oxygen concentration was reduced to zero, the wave stopped and metabolism ceased until

oxygen was readmitted. In one experiment an umbrella was kept 7 hours at zero $O_2$ concentration, then 3 hours with $O_2$ and a trapped wave, and 7 hours at zero $O_2$ concentration, during which it gave out no $CO_2$ or other acid products affecting the pH perceptibly; 30 seconds after it was taken out of the $O_2$-free chamber a trapped wave was started and this constantly increased in amplitude for 10 minutes, at the end of which time the amplitude was normal.

Oxygen was removed from sea-water in various ways, with the air-pump and agitation, by boiling, and by allowing a cassiopea to remain in it until the pulsations ceased, as seen through a peep-hole in such a way that photosynthesis was practically avoided. In no case did the analysis show less than about 0.05 c.c. per liter, but that amount probably entered with the KI and $MnCl_2$ solutions and around the ground stopper of the analysis bottle. At any rate, we should consider 0.05 c.c. to be within the limit of error of the method if no correction were made for $O_2$ in the reagents.

The variation in metabolism after removal of the manubrium and initiation of a trapped wave is shown in table 21. The diameter of the umbrella was 11.5 cm. at the beginning of the first experiment and at the beginning of each experiment the pH was 8.2 and the $O_2$ per liter 4.5 c.c. It is evident that the metabolic rate may vary rapidly for 3 hours after the manubrium is removed and the trapped wave is started: therefore, in the subsequent experiments the umbrella was not placed in the respiration chamber until these 3 hours had passed. The same umbrella used in the above experiments but 21 hours after the operation was used to determine the effect of reduced oxygen concentration. The average $O_2$ concentration during the experiment was 1.5 c.c. per liter and the $O_2$ used per hour 1.03 c.c., being a decline of 20 per cent in rate of oxidation, with a reduction of the oxygen-concentration to about half its original value. This and some later experiments are as shown in table 22.

These determinations show that oxidation is reduced about 20 per cent when the $O_2$ concentration is reduced about 50 per cent; or the oxidation increases about 25 per cent when the $O_2$ concentration is increased about 100 per cent.

The above experiments show that the rate of oxidation varies with the tension of oxygen in the sea-water constantly circulated against the surface of the epithelium in which oxidation takes place. In the total absence of oxygen no measurable quantity of $CO_2$ or other acid products are given out, and we may infer that the metabolism is suspended. If oxygen is readmitted after a suspension of the metabolism for 7 hours, the rate of metabolism rises apparently to the normal within 10 minutes. No anaërobic processes were detected during absence of oxygen for 7 hours, but in the absence of oxygen for 16 hours, anaërobic or hydrolytic processes take place. No evidence was found

to indicate that these anaërobic processes constituted the metabolism of the cassiopea. On the contrary, a great multiplication of bacteria was associated with them, and the cassiopea was partly dissolved and

TABLE 21.

| Hours after operation. | $O_2$ used per hour. | Revolutions of wave per second. |
|---|---|---|
| | c.c. | |
| 0 | 1.65 | 1.60 |
| 2 | 1.55 | 2.00 |
| 3 | 1.30 | 2.22 |
| 4 | 1.30 | 2.22 |
| 5 | 1.30 | 2.22 |
| 20 | 1.30 | 2.22 |

TABLE 22.

| $O_2$ used per hour. | |
|---|---|
| At 3.3 c.c. $O_2$ per liter. | At 1.5 c.c. $O_2$ per liter. |
| 1.3 | 1.03 |
| 1.3 | 1.00 |
| 1.4 | 1.10 |
| 1.48 | 1.15 |
| 1.44 | 1.25 |
| 1.35 | 1.05 |

could not be revived by readmission of oxygen. We may assume that oxygen protects the cassiopea from the attacks of bacteria (probably anaërobes). Since the bacteria enter from the surface, it seems probable that the cassiopea might live indefinitely on so small a supply of oxygen that it is used in the superficial cells as fast as it diffuses into them, and none reaches the deeper cells. If this be true, the variation in oxygen consumption with variation of supply might be the expression of a variation in the number of cells receiving oxygen. In other words, this would be a diffusion phenomenon.

Another hypothesis is that the tension of oxygen at the seat of oxidation affects the rate. Warburg has shown that cell oxidation is associated with structure and that no enzyme solution has been obtained that will account for the vital oxidation of foodstuffs. If the structure or surface responsible for the oxidations is designated as the catalyst, it seems possible that the tension of oxygen in the immediate vicinity of the catalyst influences the rate. This influence of tension on rate might still be a diffusion phenomenon, since the $O_2$ must diffuse toward the structure-catalyst or oxidase molecule.

Owing to the excellent review of the literature on the subject of this paper by Krogh, it seems unnecessary to multiply references. Roughly speaking, and within physiological limits, animal oxidation is about doubled with 10° rise in temperature, and this is shown here to be true of *Cassiopea*. In other words, oxidation is an exponential function of the temperature as expressed in the following equation:

$$V_t = V_o \times 2^{\left(\frac{t}{10}\right)}$$

where $V_t$ is the velocity of oxidation at $t°$ and $V_o$ at 0°. This relation holds approximately true for a number of chemical reactions and is supposed to be due partly to change in diffusion-rate and partly to loosening of bonds in the reacting molecules and to ionization. Diffusion depends on viscosity and tension (osmotic pressure). A fall of

temperature from 30° to 20° increases the viscosity of water about 25 per cent, and of a 40 per cent sucrose solution 42 per cent, and of a 3 per cent gelatine solution 1,000 per cent (von Schroeder). The increase in viscosity of gelatine, however, does not cause a proportionate decrease in diffusion. We may assume that this fall of temperature may possibly cause about 30 per cent decrease in diffusion of $O_2$ within the cell, due to viscosity alone. Tension is proportional to the absolute temperature. Although diffusion accounts for only about a third of the change in rate of oxidation with temperature, it is undoubtedly a factor. Since diffusion affects oxidation and concentration-gradient affects diffusion, it seems very probable that concentration of $O_2$ should affect oxidation, even though every cell received some oxygen.

Krogh interprets the experiments on warm-blooded animals as showing increased oxidation with increased oxygen tension, and reviews the work of Thunberg, showing the same effect to a greater degree on cold-blooded animals. Henze (1910*a*) found that the oxidation-rate of sea-anemones and annelids varies with $O_2$ concentration (and of nudibranchs at low concentrations) and supposed that only a varying fraction of the cells received oxygen; his tables show that the oxidation-rate of crustacea and jelly-fish fell rapidly with time, but that in one series of determinations on *Pelagia*, the oxidation-rate varied reversibly with $O_2$ concentration. In order to reduce the diffusion effect, he kept sea-urchin eggs agitated in sea-water and found that the oxidation-rate apparently increased about 8 per cent on doubling the $O_2$ concentration. Henze attributes this apparent difference in respiration to faulty technique, but since the experiments have not been repeated with improved technique, we may assume that a real difference exists.

It is interesting to compare the metabolism of *Cassiopea* with that of jelly-fish studied by Vernon. Since only the living cells metabolize, it would be an advantage to know the proportion of cellular tissue to the body-weight, but there is no data on this subject. The skeletal structure, mesoglœa, contains less organic matter than the cells, and hence the percentage of organic matter in the body is a partial indication of the cellular mass. The proportion of mesoglea increases with the size of the individual within the same species, but there can be no

TABLE 23.

| Species. | Weight of individual. | Cubic centimeters $O_2$ per hour. | |
|---|---|---|---|
| | | Per kilo body. | Per kilo organic matter. |
| | *gm.* | | |
| Cassiopea xamachana.... | 100 | 12.5 | 1,040 |
| Carmarina hastata..... | 39 | 7.7 | 2,025 |
| Cestus veneris..... | 70 | 3.75 | 1,562 |

strict comparison between different species in this regard, and therefore the comparison is very crude. The cubic centimeters of $O_2$ per hour per kilogram of body-weight and per kilogram of organic matter (=dry weight−weight of salts in equal volume of sea-water) at 20° is given in table 23. The agreement is about as close as could be expected.

Vernon has compared the metabolism (per unit weight of organic matter) of jelly-fish, molluscs, tunicates, and vertebrates, and shown it to be remarkably constant. Krogh (omitting jelly-fish, but including eggs and insects) obtained the greatest differences when the total body-weights were used, but the differences probably do not exceed the differences in water-content and in muscular activity. He found the metabolism of a young dog with body-temperature lowered to 20° during the experiment to be greater than that of cold-blooded animals at the same temperature; but if we calculate the metabolism of the average dog for 20°, using a reasonably high temperature coefficient, the agreement is more satisfactory. We should not expect close agreement unless water and mineral salts and fibrous tissue are excluded from the weight and the activity of the nervous system is abolished. The chief factor in lowering the metabolism of hibernating mammals is probably the fall in body-temperature (the body-temperature may be as low as 6°).

It seems probable that the chief distinction in the calorimetry of warm-blooded and cold-blooded animals is in insulation (sensitivity to cold being the regulating factor). All warm-blooded animals are air-breathing, and air brings much oxygen and takes away little heat. The center of a cluster of bees in winter may be 40° above that of the air bathing it.

The heat-production in a 100-gram cassiopea at 30° is sufficient to raise its body-temperature 0.14° per hour above that of the surrounding water, but no such difference in temperature has been observed, because the heat generated is conducted away by the water bringing the oxygen. I found that a fish weighing 1.4 grams used 0.825 c.c. $O_2$ per hour at 30°, which is sufficient to raise its body-temperature about 3° per hour, but during this time it was required to breathe 400 c.c. of sea-water, even though it removed half of the oxygen from water saturated with air at this temperature. The water circulating through the gills could remove the heat generated if the body-temperature were 0.01° above that of the water. Since the fish probably removed much less than half the oxygen from the water in one passage through the gills, the body-temperature was probably much less than 0.01° above that of the water. Rogers and Lewis could detect no difference between the body-temperature of fish, salamanders, clams, and earthworms and the water in the thermostat in which they were placed, after they had been in the thermostat long enough for equilibrium. They used a thermo-couple, and one division of the galvanometer scale corresponded to 0.0042°.

It was shown that the metabolism of *Cassiopea* is proportional to its surface and not to its weight ($W$), but to $W^{\frac{2}{3}}$. This is due to the fact that the metabolism is confined to the living cells and that these constitute a superficial epithelium, whose thickness is about the same in cassiopeas of the range of sizes studied. We might use these results in an attempt to explain the so-called surface-law of warm-blooded animals. Dreyer, Ray, and Walker have shown that the blood-volume and cross-sections of the aorta and trachea are proportional to $W^{\frac{2}{3}}$ (or surface). If animals were of the same shape (internally as well as externally), the cross-sections of all organs would be proportional to $W^{\frac{2}{3}}$, but the blood-volume would be proportional to the weight ($W$). If the blood-volume is proportional to $W^{\frac{2}{3}}$, the whole circulatory system would be nearly proportional to $W^{\frac{2}{3}}$, and owing to the close relation between the lungs and the blood the volume of the lungs would be nearly proportional to $W^{\frac{2}{3}}$. The volume of the skin may be proportional to $W^{\frac{2}{3}}$ and the volume of the wall of the alimentary tract nearly so. The nerve, muscle, and glandular tissues are excitable, and hence their metabolism must vary. Variable components may be excluded from basal metabolism by definition, but can not all be eliminated in making measurements. Only the skeleton can be said to have a constant metabolism proportional to $W$, and since the red bone-marrow produces blood (erythrocytes) and this is proportional to the surface, the metabolism of some of the bones may be nearly proportional to the surface. Benedict has shown that great variations from the surface law exist, and hence it may be only accidental.

The fact that the excitable tissues metabolize more per unit weight in small animals than in large (*i. e.*, proportional to a smaller power of $W$ than unity) is true, not only for warm-blooded animals, but also for cold-blooded animals, to which the teleological principle of the surface law (in relation to heat regulation) does not apply. It seems possible, however, that the chief conditions necessary for the evolution of temperature-regulation in animals were: (1) air breathing; (2) large body size; (3) sensitivity to low temperatures; (4) variation of activity of excitable tissues with size; and (5) epithelial type of architecture, 4 and 5 being more characteristic of cold-blooded animals.

It is hoped that the fact that metabolism varies with $O_2$ tension may explain the increase in metabolism in certain types of acidosis. Lusk and Richie have shown that certain amino acids have a specific dynamic action and Benedict asserts that it has been demonstrated that there is a distinct increase in the basal metabolism with the acidosis resulting from the ingestion of a carbohydrate-free diet. It is not assumed that amino acids dissociate enough H ions or neutralize enough base to cause acidosis, and whether there is any relation between the phenomena discussed by Lusk and by Benedict may be open to question, but it seems clear that increased metabolism may accompany acidosis.

Acidosis develops in the acclimatization to high altitudes and persists some time after the descent, during which time the subject feels more vigorous (Schneider). During acidosis the ventilation of the lungs is increased to such an extent that the alveolar air is increased, and therefore the $O_2$ in the blood-plasma is increased and that in the hemoglobin is increased if it is not already saturated. Increased respiratory movements tend to increase the heart-rate and hence the circulation, with better oxygen transfer to the tissues and increased oxidation. This effect may be small, and may be too small to account for the total increase in metabolism, but is worthy of consideration. Rasmussen has shown mild acidosis in case of the hibernating woodchuck with very much lowered $O_2$ tension of venous blood, but evidently the sensitivity of the respiratory center falls during hibernation.

It was shown by Warburg that the metabolism of sea-urchin eggs may be stimulated, but these are to be considered irritable cells in the same class with muscle. It may be that the metabolism of all cells can be stimulated, but they are not equally sensitive. Changes in hydrogen-ion concentration of the sea-water effective on sea-urchin eggs are not nearly so effective on the cells of *Cassiopea* (possibly because the pH of the sea-water changes before reaching the cells). Benedict claims that the basal metabolism of the human body may be stimulated, but it is difficult to estimate basal metabolism on account of the unavoidable activity of some excitable organs. Cutting the nerves is of no advantage, since Langley and Itagski showed that the oxygen consumption of denervated muscle is much greater than that of normal resting muscle. What cells are stimulated in Benedict's experiments is not clear. He adds that changes in the pulse-rate accompany changes in the basal metabolism, and thus admits that irritable cells of the complex neuro-muscular organization of the body are concerned in the phenomenon. If the respiratory or vasomotor centers are concerned in the increased metabolism, $O_2$ tension in the tissues may be a factor. Verzár showed that resting muscle and active heart use more oxygen when there is more in the blood. The submaxillary gland used oxygen at the same rate in all experiments, but suffocation of the animal occurred when the oxygen tension in the gland was about 40 mm. Rasmussen (see also Dubois) has shown that the oxygen concentration of the venous blood of marmots (woodchucks) is lowered during hibernation, although the oxygen capacity of the blood remains the same. This shows that the $O_2$ tension of the blood is lowered both by fall in concentration and temperature, and this may be a factor in the lowered metabolism. The $O_2$ concentration of the arterial blood is not reduced, but the rate of blood-flow is very much reduced, so that less oxygen is carried to the tissues.

## ON THE CHEMICAL PRECIPITATION OF $CaCO_3$ IN SEA-WATER.*

The question of the solubility of calcite and aragonite in sea-water is a matter of interest in relation to the geology of limestone and dolomite. Murray and Hjort maintain that sea-water is so complicated a mixture that the solubility of $CaCO_3$ can not be calculated with certainty (from the law of mass action), but that the experiments of Anderson and of Cohen and Raben show that sea-water is saturated with calcite. They add (p. 181) that dolomite is less soluble than calcite in carbonated water. Their book summarizes observations showing that calcium carbonate is precipitated in shallow tropical waters, but that even shells are dissolved in the red-clay bottoms of the depths.

Mayer (1916) placed pieces of *Cassis* shell in sea-water for more than a year and found that they maintained their weight within about 0.1 per cent. The precipitation of $CaCO_3$ at Tortugas was studied by T. Wayland Vaughan, R. B. Dole, and G. H. Drew. Drew observed that a denitrifying bacillus, *Pseudomonas calcis*, obtained from the sea-water was capable of changing calcium nitrate to calcium carbonate in culture media and supposed a similar process to occur in sea-water. Since Vaughan has observed that calcium carbonate is constantly precipitating at Tortugas, Drew's hypothesis necessitates the presence of an appreciable amount of nitrates or nitrites, and I have attempted to determine them.

A half liter of sea-water was boiled in an all-glass still and the distillate collected in a series of 25 c.c. Nessler's tubes; another series of Nessler's tubes were filled with a graded series of concentrations of ammonium chloride; 1 c.c. of Nessler's reagent was added to each tube and agitated; after 15 minutes the tubes were compared colorimetrically and the ammonia recovered from the sea-water was estimated; after no more ammonia could be distilled from the sea-water, amalgamated aluminium shavings were introduced into the still and the distillation process was repeated. The ammonia recovered was formed by reduction of nitrates and nitrites. Duplicate analyses gave less than 0.01 mg. of nitrogen per liter as ammonia and less than 0.01 mg. nitrogen per liter as nitrates and nitrites. Raben found more than 10 times these quantities in North Sea water (Murray and Hjort, p. 368). Evidently *Pseudomonas calcis* and other organisms have almost completely removed the fixed nitrogen from Tortugas sea-water. The effect of this probably explains the scarcity of life in the vicinity of Tortugas as compared with colder seas (law of minimum). There is, however, a constant renewal of fixed nitrogen from the atmosphere, from the decay of organisms, and probably from water rising from the depths of the ocean. If *Pseudomonas calcis* is an important agent in the precipitation of $CaCO_3$, its action is evidently more

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intense in places where calcium salts, nitrates, and nitrites are carried from the land into the sea.

That calcium carbonate is withdrawn from surface waters of the sea is shown by chemical analyses. Dittmar found an average of 0.44 per cent less calcium in surface waters than in deeper waters. This is true, notwithstanding the fact that calcium carbonate is constantly being added to the surface waters. The drainage of the land contains an excess of calcium carbonate and flows out on the surface of the sea, where the water evaporates, leaving the excess of $CaCO_3$ in the sea-water. The action of organisms in building calcareous structures may account for a large part of the depletion of surface waters, but the precipitation of calcareous mud at Tortugas has been observed by Vaughan.

The analysis of the calcium content of sea-water requires double precipitation and filtration for separation from magnesium, and hence large samples and great care are required for accuracy. Theoretically, however, we may detect differences in calcium content by titration. Dittmar showed that sea-water is remarkably constant in composition, except for $H_2O$, calcium, and gases. The water content is inversely proportional to Cl and the gases may be eliminated by boiling after the addition of enough acid to decompose the carbonates. If we disregard carbonic acid, there is an excess of bases in sea-water—*i. e.*, the sum of the base equivalents is greater than the sum of acid equivalents. Since calcium is added to or taken from sea-water in the form of $CaCO_3$, any change in the calcium content causes an equivalent change in the excess base or alkaline reserve, as it is called by chemists. The alkaline reserve may be titrated while boiling the sea-water to eliminate $CO_2$. The exact value of the titration depends on the indicator used and the exact color of the indicator that is taken as the end-point; hence only those titrations done in the same manner can be strictly compared (see method described in first part of this paper). The alkaline reserve per liter was recorded and some titrations were made at 20° and others at 30°, but the errors due to change in volume of the sea-water is within the limits of accuracy of the method. If the sea-water is diluted with rain-water, the alkaline reserve will be lowered, but this error may be compensated by dividing by Cl. In other words, a change in the quotient of the alkaline reserve by Cl indicates a gain or loss of $CaCO_3$.

TABLE 24.

| Sea-water from— | Alkaline reserve. | Cl. | $\frac{\text{Alk. res.}}{\text{Cl}} \times 10{,}000$ |
|---|---|---|---|
| San Diego | 0.00235 | 18.7 | 1.257 |
| Wood's Hole | .00240 | 17.7 | 1.356 |
| Gulf Stream, off Miami | .0025 | 19.9 | 1.257 |
| Gulf Stream, off Tortugas | .0025 | 19.9 | 1.257 |
| Average, Tortugas, June and July | .00247 | 20.0 | 1.235 |
| Average, Key West, June and July | .00237 | 20.0 | 1.185 |

Table 24 indicates that some $CaCO_3$ has been removed from Tortugas sea-water, as compared with other sea-water, and to a greater extent from Key West sea-water. In other words, the precipitation observed by Vaughan is not due to a greater amount of calcium in Tortugas or Key West sea-water, but to local conditions which cause the precipitate to form.

According to the law of mass-action, in a saturated solution of $CaCO_3$, in sea-water at constant temperature, salinity, etc.,

$$[Ca^{\cdot\cdot}] \times [CO_3''] = \text{a constant}$$

Not all of the calcium is, however, in the form of $CaCO_3$ and $Ca^{\cdot\cdot}$, for some is undissociated $CaCl_2$, $CaSO_4$, $Ca(OH)_2$, and $CaHCO_3$. The chlorides and sulphates are constant, but $[CaHCO_3]$ and $[Ca(OH)_2]$ change with the total $CO_2$ content of the sea-water. But I have shown (McClendon, 1917*b*) that if the alkaline reserve remains constant the total $CO_2$ of the sea-water (within limits found in nature) varies inversely with the pH ($= -\log. H^{\cdot}$ concentration). Hence the determination of the pH may be substituted for that of the total $CO_2$.

The determinations I have made of the water of the Pacific and North Atlantic showed the pH to vary from about 8.1 to 8.25 and those of Dr. A. G. Mayer in the Pacific showed only a little wider range (table 11). Earlier observations at Tortugas gave the same range, but my more extended observations in this summer of 1917 show the inadequacy of a few determinations. The pH is influenced by plant and animal life and rises at Tortugas to 8.35 during the day over well-lighted bottoms rich in vegetation, and falls to 8.18 during the night. It may be said, therefore, that conditions in shallow water over eel-grass or other seaweed or corals (with symbiotic algæ) favor the precipitation of $CaCO_3$.[1]

The question arises whether the occasional high pH of Tortugas sea-water is sufficient to explain the precipitation of $CaCO_3$, or whether nuclei for the separation of the solid phase are necessary. A large amount of $CaCl_2$ may be added to sea-water without causing a precipitation. If the pH is increased by the addition of NaOH, the result depends on the speed at which the alkali is added. If the NaOH is added suddenly in the form of a strong solution, colloidal precipitation membranes form about the drops and if the membranes are broken by shaking or stirring, a great mass of $Mg(OH)_2$ is included in the precipitate. If a very dilute solution of NaOH is added very slowly, $CaCO_3$ possibly contaminated with $Mg(OH)_2$ is precipitated. The exact pH at which precipitation first occurs can not be determined by this method, as the first precipitation occurs before the solutions are mixed and the crystals thus formed serve as nuclei for further precipita-

[1]It would be interesting to know whether corals and calcareous algæ deposit as much $CaCO_3$ in the dark as in the light. Corals from deep water are smaller, more fragile, and deposit less $CaCO_3$ than those of shallow water, but the same is true of animals without symbiotic algæ. The deposition is, however, related to the pH, since Palitzsch has shown that the pH decreases with depth.

tion. If Tortugas sea-water is kept in glass bottles, precipitation occurs on the glass while the pH of the water is within the natural limits, but the pH at the glass surface is higher, due to solution of glass.

Although the pH at which precipitation would occur without nuclei for the separation of the solid phase may be practically impossible to determine, the final equilibrium with an abundance of nuclei is not a difficult problem. Calcite and aragonite crystals to serve as nuclei were produced by the methods of Johnston, Merwin, and Williamson. The crystals were examined under the microscope and tested with cobalt-nitrate solution. These observations, together with the mode of preparation, leave little doubt that the crystals actually were calcite and aragonite. Under the microscope an occasional calcite crystal could be found among the aragonite crystals, but the number was not sufficient to affect the cobalt-nitrate test. These calcite crystals seemingly grew slightly during the experiments, but apparently no new ones were formed. To determine the equilibria, crystals were mechanically stirred or shaken with sea-water in "nonsol" flasks, 6 to 14 hours at 30°; then the pH and alkaline reserve were determined.

The results of agitating 100 grams of calcite crystals with a liter of sea-water until equilibrium was approximately reached also appear in figure 7. The alkaline reserve is measured on the ordinate and the pH on the abscissa. This shows that sea-water of the surface of the oceans of the whole world is supersaturated in respect to calcite. We may therefore conclude that suitable nuclei for the precipitation of calcite are absent or deficient in number. The solubility of crystals varies inversely with their size, but after they have attained sufficient size to be readily examined with low powers of the microscope further increase has an unappreciable effect on solubility. But such crystals, if present, would rapidly gravitate to the bottom of the sea; hence the absence of nuclei for precipitation of calcite is what one might expect.

Aragonite is said to be about 10 per cent more soluble than calcite, but no difference in the point of equilibrium of the two substances with sea-water was detected in these experiments (fig. 8). This may be explained by the fact that a few calcite crystals were mixed with the aragonite, equilibrium was only approximated, and there were slight errors in the determinations.

During the rough weather, white calcareous mud is stirred with the sea-water at Key West and to a lesser extent at Tortugas, and it was thought possible that the mud granules might form nuclei for precipitation and explain the low alkaline reserve at Tortugas and lower alkaline reserve at Key West. On agitating white calcareous mud, dredged from the bottom, with sea-water, no definite equilibrium was reached, even at the end of 4 days. If the alkaline reserve was first lowered by removal of some $CaCO_3$, it remained lower than if shaken with calcite, and if normal sea-water was used the alkaline reserve remained higher than with calcite. It was thought possible that the

grains were covered with an impenetrable film of organic matter; so some mud was dried and powdered in a mortar to break the pieces and form fresh surfaces, but similar results were obtained with this.

If mud was mixed with an equal weight of calcite, the results were the same as with pure calcite. This mud and calcite on standing in sea-water for 30 days had not all changed to calcite. All these facts

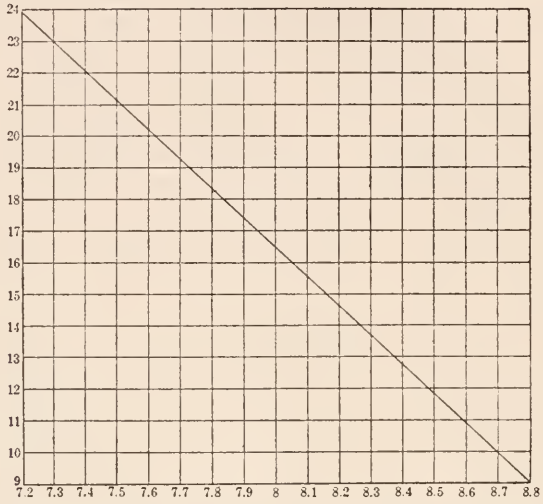


Fig. 7.—Equilibrium of calcite with Tortugas sea-water. The pH is marked on the abscissa and the alkaline reserve × 10,000 on the ordinate.

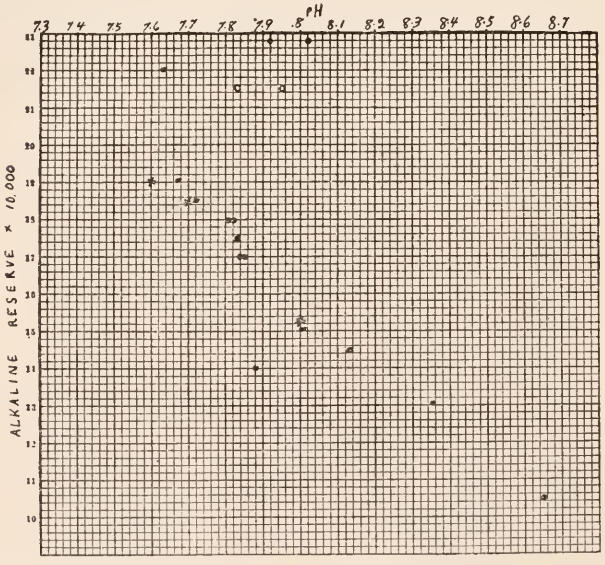


Fig. 8.—The equilibrium of $CaCO_3$ with Tortugas sea-water. Calcite is denoted by black rhombs, aragonite by rosettes, calcareous mud by black circles (no equilibrium), mud and calcite by black dumb-bells, and pulverized coral by white circles.

tend to show that the particles in the mud are in some way retarded or prevented from getting into equilibrium with the water.

In order to be sure of clean surfaces of natural calcareous substances, a specimen of coral, *Mœandra clivosa*, was ground and powdered in a mortar and agitated with sea-water in the same manner as in previous experiments. The results were similar to those with mud (fig. 8).

There seems to be a more soluble form of calcium carbonate (the $\mu CaCO_3$ of Johnston), but since it can not be obtained in a pure state no attempt was made to prepare it. One experiment, however, was made with a precipitate of $CaCO_3$ that appeared as spherical grains under the microscope. It was agitated for 12 hours with sea-water and the alkaline reserve was 0.0022 at pH 7.95. No further experiments were made to determine whether equilibrium had been approximated.

These experiments clearly show that the surface water of the sea is a supersaturated solution of $CaCO_3$; and it is only necessary to introduce calcite crystals in order to cause considerable precipitation of this substance. Precipitation goes on in the bodies of organisms in the surface waters of all seas. The precipitation observed by Vaughan at Tortugas is very finely divided, but whether it was formed in the bodies of minute organisms, which subsequently died, has not been determined. Such particles might slowly grow, since the agitation of them with sea-water was found to take a trace of $CaCO_3$ out of the water. Small crystals have been seen in the bodies of *Protista* and, whether they are $CaCO_3$ or not, they might form nuclei for the precipitation of $CaCO_3$ if released into the sea-water.

TABLE 25.

| Sea-water. | pH. | Total $CO_2$. | Alkaline reserve. | Calculated loss of $CO_2$. | |
|---|---|---|---|---|---|
| | | | | From total $CO_2$. | From alkaline reserve. |
| Before agitation with calcite.. | 8.2 | 44.5 | 0.0025 | 6 | 6.72 |
| After agitation with calcite... | 7.67 | 38.5 | .0019 | ... | .... |
| Before agitation with calcite.. | 8.25 | 43.8 | .00250 | 6.8 | 7.27 |
| After agitation with calcite... | 7.72 | 37 | .00185 | ... | .... |

In some experiments in liter flasks of resistance glass, filled to the neck (and hence admitting but slight loss of $CO_2$), the pH and alkaline reserve were determined immediately before and after agitation with calcite. The loss of $CO_2$ from the sea-water was estimated in two ways: (1) the remaining $CO_2$ was calculated from the pH and alkaline reserve; (2) the loss of $CaCO_3$ was calculated from change in alkaline reserve.

In table 25, the agreement is very striking, in view of the probable error in determination of pH and the liability to loss of $CO_2$ from the water surface in the neck of the flask, agitated by the rotary stirrer. If the pH of sea-water should be maintained (by the action of plants)

at 8.2 while it was agitated with calcite crystals, the loss of $CaCO_3$ would be about 0.001 N, or 0.0005 M, or 0.1 gram per liter. This would cause a deposit of 10 kg. per square meter of bottom in water 100 meters deep. This would cause a lowering of the total calcium content of Tortugas sea-water by about 4.5 per cent.

The actual precipitation of $CaCO_3$ was most noticeable in the Marquesas lagoon. At 4 p. m., July 30, the pH was 8.46 and there was a precipitate of $CaCO_3$ coming down in the water and incrusting the eel-grass.

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